Eesti Maaülikool
Estonian University of Life Sciences

VARIATION IN THE HABITAT REQUIREMENTS OF POLLINATING INSECTS IN SEMI-NATURAL MEADOWS

TOLMELDAJATE ELUPAIGANÕUDLUSTE MITMEKESISUS POOLLOODUSLIKES KOOSLUSTES

AVE LIIVAMÄGI

A Thesis for applying for the degree of Doctor of Philosophy in Environmental protection

Väitekiri
filosoofiadoktori kraadi taotlemiseks keskkonnakaitse erialal

Tartu 2014

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Opponent: Prof. **Miska Luoto**
Department of Geosciences and Geography
University of Helsinki
Helsinki, Finland

Supervisor: Prof. **Valdo Kuusemets**
Institute of Agricultural and Environmental Sciences
Estonian University of Life Sciences
Tartu, Estonia

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IV. **Liivamägi, A.**, Kuusemets, V., Luig, J. & Kask, K. 2013. Changes in the distribution of Clouded Apollo *Parnassius mnemosyne* (Lepidoptera: Papilionidae) in Estonia. Entomologica Fennica 24 (3): 186-192.

V. Kuusemets, V., Meier, K., Luig, J. & **Liivamägi, A.** 2005. Habitat and landscape structure of Clouded Apollo (*Parnassius mnemosyne*). Kuchn, E., Thomas, J., Feldmann, R. & Settele, J. (Eds.) Studies on the Ecology and Conservation of Butterflies in Europe. Vol.1. General Concepts and Case Studies. Pensoft Publishers, Sofia-Moscow, p 18-21.

Contributions

	I	II	III	IV	V
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AL – Ave Liivamägi; ID-F – Isabel Diaz-Forero; JL – Jaan Luig; KK – Kadri Kask (former name Kadri Meier); MM – Marika Mänd; TK – Tanel Kaart; VK – Valdo Kuusemets

ABBREVIATIONS

AREA	Patch area
AREA_MN	Mean patch area of forest
AvCoverFP	Average percent cover of the plants in the flowering stage
AvGrassH	Average vegetation height
ED	Edge density
ED_LAND	Edge density at landscape level
FRAC	Fractal dimension index
GIS	Geographic information system
IJI	Interspersion and juxtaposition index
PArLand	Proportion of patches that are arable land
Pbrushw	Proportion of patches that are brushwood
PForest	Proportion of patches that are forest
PHumSet	Proportion of patches that are human settlement
PMeadows	Proportion of patches that are meadow
PERIM	Perimeter of the patch
PLS	Partial least squares
PRD	Patch richness density
SHAPE	Shape index
SHDI	Shannon's diversity index
SRFFlowPlants	Species richness of flowering plants

1. INTRODUCTION

The pollinating insects considered in this thesis are bumblebees (Hymenoptera: Apidae, *Bombus* spp.), butterflies, and day-active moths (Lepidoptera).

Many pollinating insect species have undergone serious declines in both abundance and range extent in most European countries (Goulson *et al.* 2008, Warren & Bourn 2011). A recent report (van Swaay *et al.* 2013) states that the population of grassland butterfly species decreased by almost 50% from 1990 to 2011. A review of bumblebees (Kosior *et al.* 2007) declared the extinction of four species and indicated that 30% of species became threatened during the second half of the 20th century in Western and Central Europe. There is evidence that specialist species have declined more rapidly than generalist species (van Swaay *et al.* 2006, Williams & Osborne 2009). Furthermore, it has been found that plant species that are reliant on the declining pollinators have also experienced a decrease (Biesmeijer *et al.* 2006, Carvell *et al.* 2006, Wallisdevries *et al.* 2012, Carvalheiro *et al.* 2013).

Several factors have been suggested as possible contributors to these declines, and there are differences for certain taxa and regions. For butterflies and moths, the main drivers are deterioration of habitat quality (Mortelliti *et al.* 2010), increased fragmentation of habitat patches (Krauss *et al.* 2010), increased agricultural intensification (Stoate *et al.* 2002; Benton *et al.* 2003; Luoto *et al.* 2003), and climate change (Parmesan 2006; Maes *et al.* 2010). For bumblebees, the factors that threaten a species or population are intensification of agricultural practices (homogenisation of landscape, loss of flower-rich habitats), application of chemical preparations, more intensive cutting or grazing of grasslands, reduced use of favourite forage plants (*Fabaceae*) for bumblebees, and climate change (Goulson *et al.* 2008, Williams & Osborne 2009). Obviously, the interaction of all these factors threatens butterflies, moths, and bumblebees around the world (Goulson *et al.* 2008, Shreeve & Dennis 2011).

Bumblebees, butterflies, and moths have a key function through their role in plant reproduction (especially bumblebees). These organisms are important parts of the food-chain and are therefore a valuable indicator of ecosystem health and functionality (Parmesan 1996, Thomas 2005).

Furthermore, these species are excellent model organisms for studying environmental changes and the status of ecosystems because their ecology is particularly well known: they are easy to identify, even for amateurs, and are thus easy to monitor; they have annual life cycles and thus quickly respond to environmental changes; and there are many specialist species among butterflies and bumblebees that depend on certain habitat requirements or food plants and are therefore influenced by the landscape composition and configuration (Kremen *et al.* 1993, Bourn & Thomas 2002, Hatfield & LeBuhn 2007). Considering these above-mentioned facts, the conservation of butterflies, moths, and bumblebees and their habitats may also benefit other taxa. Therefore, both insect groups have been increasingly recognised as valuable environmental indicators (Thomas 2005), and many studies are thus concentrating on the investigation of the relationships between species diversity patterns and their preferred habitat conditions in different landscape structures at different spatial scales (Sjödin *et al.* 2008, Ekroos *et al.* 2010, Öckinger *et al.* 2012).

In Estonia, land-use change can be considered a major driver for shifts in butterfly and bumblebee species compositions. Similarly to other European countries, the traditional extensive agricultural practice is decreasing in Estonia. In general, the area of semi-natural grasslands in Estonia has decreased from 1,571,000 ha in 1939 to 130,000 ha in 2006 (Kukk & Sammul 2006). Additionally, the proportion of forest has increased substantially (from 14% to 42%) during the 20th century (Palang *et al.* 1998).

The order of Lepidoptera is represented in the fauna of Estonia by approximately 2400 species. There are approximately 123 butterfly (Papilionoidea and Hesperioidea) species, some of which are rare immigrants (Jürivete & Õunap 2008). Of these 123 species, eight species are protected by the national protection act (Nature Conservation Act), and seven species are protected by the EU Habitat Directive. The Estonian Red List of Threatened Species includes 32 species of butterflies (Papilionoidea and Hesperioidea), of which 22, six, and four are classified as *data deficient*, *least concerned* and *not applicable*, respectively (Lilleleht 2008). In the case of bumblebees, the genus *Bombus* is represented in the fauna of Estonia by approximately 29 species, of which seven are parasitic species (cuckoo bumblebees) of the former subgenus *Psithyrus* of bumblebees. Eighteen bumblebee species are legally protected by Nature Conservation

Act. In the year 2008, there were nine bumblebees included in the Estonian Red List of Threatened Species, and all of these were classified as *data deficient* (Lilleleht 2008).

Both insect groups are well studied in Estonia, and the distribution of butterfly and moth species is rather well documented. There are nation-wide coarse scale distribution maps of Estonian Lepidoptera (Jürivete & Õunap 2008). In contrast to butterflies and moths, there are no distribution maps of bumblebees. However, there is need for a more detailed estimation of the distribution changes and abundances of the flower-visiting insects of interest.

To mitigate the loss in the biodiversity of butterflies, moths, and bumblebees, it is important to increase our knowledge of the ecology of the different species, to analyse their distributions and statuses, and to study the causes of their declines in different landscapes and geographical ranges.

The aim of the thesis was to evaluate the relative importance of patch and landscape factors for butterflies, day-active moths, and bumblebees in forest-dominated landscapes in north-eastern Estonia. The effects of the habitat patch characteristics (area, habitat quality in terms of vegetation parameters) and the surrounding landscape composition (e.g., area of meadows, forests, and arable land) and configuration (e.g., edge density, Shannon's diversity index) on the species richness and abundance were analysed at various spatial scales. Additionally, the distribution and general habitat requirements of the endangered butterfly species Clouded Apollo (*Parnassius mnemosyne* Linnaeus 1758) were assessed. The species is a habitat and larval host plant specialist. Due to its specific requirements associated with environmental and habitat conditions, Clouded Apollo can serve as an indicator (key species) of the state of semi-natural meadows. Furthermore, due to its conspicuous appearance, this butterfly can be used as a flagship species for the conservation of the biodiversity of pollinating insects and other taxa.

2. REVIEW OF THE LITERATURE

2.1. Relationships between habitat patch characteristics and pollinating insects

The existence and availability of a suitable habitat is essential for the survival and successful reproduction of all species. A habitat is a species-specific unit composed of abiotic and biotic factors that are favourable for a particular species. A habitat is frequently regarded as a vegetation category or biotope (Dennis *et al.* 2006). A patch is relatively homogeneous nonlinear area that differs from its surroundings (Lindenmayer & Fischer 2006). In principle, a habitat patch is a discrete area of suitable vegetation type that is used by a species for various activities, including occupancy, breeding, foraging, and overwintering. In a given habitat patch, various species can coexist because different species have different requirements.

The influence of the habitat patch characteristics (particularly quality and area) on species richness (number of species) and abundance (number of individuals) has received much attention in spatial ecology, because it is important to determine and understand these relationships for effective biological conservation. There are some known theories predicting interactions between habitat characteristics and species richness. For example, the island biogeography and the metapopulation theory both predict that the richness and total abundance of a species increase with an increase in the habitat patch area (MacArthur & Wilson 1967, Hanski 1999). Several studies have confirmed this relationship for bumblebees and butterflies (e.g., Öckinger *et al.* 2011, Soga & Koike 2012), although the evidence for bumblebees is scarce (Potts *et al.* 2010).

Öckinger & Smith (2006) showed that the species richness of butterflies is higher on larger grasslands. A study in southern Poland also showed that the butterfly species richness and abundance are positively affected by the patch size (Rosin *et al.* 2012). In addition, Krauss *et al.* (2003) found that the overall butterfly density increases with an increase in the area. Furthermore, it has been declared that the number of habitat specialist butterflies increases significantly with increasing area (Steffan-Dewenter & Tscharntke 2000, Krauss *et al.* 2003). Similarly, Brückmann *et al.* (2010) found that the species richness, density, and abundance of habitat-specialist butterflies are significantly higher in large compared with small habitat patches.

For bees, Jauker *et al.* (2013) showed that the habitat area is important factor explaining the species richness patterns of wild bees in calcareous grasslands. Furthermore, these researchers concluded that large bee species (bumblebees) with greater mobility are less susceptible to the effects of habitat loss. Similarly, Bommarco *et al.* (2010) found that bumblebees are less sensitive to patch size and thereby presumably less sensitive to habitat loss.

Other studies report the importance of small habitat fragments on the species richness and abundance of butterflies (Tscharntke *et al.* 2002b, Kuussaari *et al.* 2007, Kumar *et al.* 2009). Several studies have not found an effect of habitat patch area on the species richness or abundance of butterflies (Binzenhöfer *et al.* 2005) and bumblebees (Hatfield & LeBuhn 2007).

An increase in the habitat area is closely related to an increase in habitat quality (diversification of resources), which is also an important factor describing the species-habitat relationship (Hanski 1999). Theoretically, a habitat patch of high quality supports more species than a low-quality patch.

There are various determinants for habitat quality (host plant abundance, number of plant species in flower, abundance of flowers, vegetation structure, nesting resources, hibernation structures, etc.) depending on the species resource requirements. Unfortunately, it is hard to define all of the resources for a species or a group of species because some aspects of the ecology of the species of interest are still unknown or there are inconsistencies in some issues. Furthermore, there is evidence that the same species in different geographical regions or landscapes have different habitat requirements (e.g., preferences for host plant species).

In the case of butterflies, moths, and bumblebees, forage resources (larval host plant and nectar supply for butterflies, nectar and pollen for bees) constitute one of the main resources determining habitat quality. Many studies have shown that butterfly and bumblebee species richness and abundance are highly correlated with the abundance and richness of floral resources (Skórka *et al.* 2007, Marini *et al.* 2009, Mortelliti *et al.* 2010, Potts *et al.* 2010, Rosin *et al.* 2012, Wallisdevries *et al.* 2012). Bergman *et al.* (2008) found that the nectar supply (flower abundance) is

positively correlated with butterflies. Öckinger & Smith (2006) showed a significant relationship between butterfly species richness and habitat quality measured by the abundance of flowers. Similarly, Kumar *et al.* (2009) found that the number of butterfly species recorded is strongly positively correlated with the plant species richness. For bumblebees, Rundlöf *et al.* (2008) found that the local abundance of forage resources is significantly positively associated with bumblebee abundance. Similarly, Kleijn & Van Langevelde (2006) showed that the bumblebee species richness at the local scale is positively correlated with the habitat quality measured as the number of inflorescences. In addition, Pywell *et al.* (2005) found that a high abundance of nectar and pollen resources has positive effects on the bumblebee species richness and abundance.

As well as floral resources, the vegetation structure has been shown to be associated with butterfly and bumblebee species richness and abundance (Öckinger & Smith 2006, 2007). The importance of the vegetation structure is derived from its attribute to create microhabitats (for nesting, breeding, and foraging) and transform the microclimate. The vegetation type and structure can change through the natural processes (succession) or human activities (agriculture, forestry). There are severely threatened vegetation types (semi-natural grasslands) that harbour species-rich butterfly and bumblebee communities and require a variable intensity of human-related intervention (grazing, mowing). The response of bumblebees and butterflies to grazing is, however, highly dependent on the intensity of grazing. Intermediate levels of mowing or grazing can increase plant species richness and thereby benefit the diversity of flower-visiting insects (Carvell 2002). The intensive management of grasslands with a decrease in floral abundance and diversity may have negative effects on the populations of pollinating insects (Kruess & Tscharntke 2002, Winfree *et al.* 2009).

Moreover, the abandonment of semi-natural grasslands (cessation of traditional management regimes) also alters the communities of flower-visiting insects. A case study by Stefanescu *et al.* (2009) demonstrated that there were distinct changes in the composition of butterfly fauna in hay meadows seven years after their abandonment (habitat specialists were replaced by generalists). A similar trend has been identified by many researchers (Kuussaari *et al.* 2007, Pöyry *et al.* 2009, Ekroos *et al.* 2010, Öckinger *et al.* 2010).

2.2. Relationships between landscape characteristics and pollinating insects

The spatial distribution of species and the availability of a suitable habitat are affected by the composition and configuration of the surrounding landscape. Several recent studies have investigated pollinating insect diversity in relation with various landscape factors (Tscharntke *et al.* 2002a, Dauber *et al.* 2003, Krauss *et al.* 2003, Öckinger & Smith 2006, Davis *et al.* 2007, Krämer *et al.* 2012). Similarly, the importance of woody vegetation on several butterfly and bumblebee species has been recently demonstrated (Kreyer *et al.* 2004, Kuussaari *et al.* 2007, Winfree *et al.* 2007, Bergman *et al.* 2008, Marini *et al.* 2009, Krämer *et al.* 2012). In the study conducted by Marini *et al.* (2009), the proportion of woody vegetation was found to have the strongest effect on the butterfly species richness at the local spatial scale. The significance of the forest disappeared with an increase in the spatial extent. Similarly, Krämer *et al.* (2012) found that the number of habitat specialist butterflies increases with an increase in the area of forest habitat surrounding the habitat patch. In addition, Öckinger *et al.* (2012) showed that the species richness of butterflies is highest in forest-dominated landscapes. Taki *et al.* (2007) found that the bumblebee abundance and species richness is positively related to the forest cover.

The importance of the meadow habitat in the surrounding landscape is also an important factor for pollinating insects. Öckinger & Smith (2006) showed that the species richness of butterflies is higher in grassland sites situated in landscapes consisting of a high proportion of grasslands. The proportion of meadows in the surrounding habitat has been found to have a positive influence on the species richness and abundance of bumblebees (Hatfield & LeBuhn 2007). In contrast, the proportions of meadows in the surrounding landscape do not invariably enhance the local species richness (Krauss *et al.* 2003, Bergman *et al.* 2008).

In addition to the effects of natural and semi-natural habitats in the surrounding landscape on the species richness and abundances of flower-visiting insects, the impact of human-influenced land cover types, such as arable land and human settlements, on bumblebees and butterflies have been studied. There is evidence that intensified agricultural areas have negative effect on butterfly diversity (Flynn *et al.* 2009, Ekroos *et al.* 2010). However, Ekroos *et al.* (2010) found a threshold value (60%) above which the arable land cover has stronger negative effect on butterfly

diversity. A study by Ökinger *et al.* (2012) focussing on the relationships between landscape matrix and species richness of butterflies in grassland fragments demonstrated that the number of species is lower in arable than in forest landscapes. For bumblebees, the arable land may provide additional foraging resources. It has been found that flowering crops offer various resources for bumblebees and therefore support bee communities (Bäckman & Tiainen *et al.* 2002, Westphal *et al.* 2006, Winfree *et al.* 2007).

Some studies have shown that human settlements, in terms of flower-rich gardens or roadside verges, in the surrounding landscape may enhance the species richness and abundance of flower-visiting insects (Saarinen *et al.* 2005, Noordijk *et al.* 2009, Goulson *et al.* 2010). For example, Goulson *et al.* (2010) found that gardens, in terms of nesting sites, support high densities of bumblebees.

The spatial arrangement of habitat patches (aggregations and connections) in a landscape is an important factor for the survival of flower-visiting insects. More fragmented habitats may reduce the dispersal and resource acquisition of species and thereby the persistence of populations in the landscape. Some authors have demonstrated that fragmented habitat patches have lower species richness than less isolated ones (Steffan-Dewenter & Tscharntke 2000, Tscharntke *et al.* 2002b). Brückmann *et al.* (2010) found that the total loss of grassland connectivity reduces the species richness of specialist butterflies. At the species level, several studies have confirmed the importance of well-connected habitat patches for the populations of the habitat specialist butterfly Clouded Apollo (Välimäki & Itämies 2003, Gorbach & Kabanen 2010). Moreover, it has been suggested that the ability of a species to migrate may be indicative of adaption. Hanski *et al.* (2002) showed that female butterflies of species adapted to a network of discrete habitat patches are more mobile than those of species adapted to a network of dense habitat patches.

In the case of bumblebees, the negative effect of the isolation of habitat patches on the species richness of bees was found by Jauker *et al.* (2009). However, this effect depended on the composition of the surrounding landscape, i.e., in landscapes with sufficient adjacent grassland cover, the species richness of bumblebees did not change. Furthermore, the same study also demonstrated that the abundance of bumblebees declined with an increase in the distance from the main habitat, irrespective of the surrounding landscape.

The effect of the isolation of habitat patches on the pollinating insects is related to their dispersal capacity, perception of the habitat, and ability to move across or through the landscape matrix. The permeability of the matrix is the result of human activity. The matrix may be comprised of elements that enhance (e.g., corridors, stepping-stone patches) or limit (e.g., certain boundaries, land-cover types) the dispersal of individuals and therefore minimise or increase the effect of habitat fragmentation (Öckinger & Smith 2008, Dover & Settele 2009, Prevedello & Vieira 2009).

Several studies have demonstrated how butterfly species avoid habitat edges or prefer to move along the edges (Haddad 1999, Roland *et al.* 2000, Ries & Debinski 2001, Auckland *et al.* 2004). Conversely, there are some examples in which habitat edges (the tree stands) have no significant impact on the movement of the butterfly species (Konvička & Kuras 1999, Välimäki & Itämies 2003). Furthermore, it has been argued that the movements of butterfly species adapted to live in open habitats are more influenced by physical barriers, such as forests and tree-lines (Ries & Debinski 2001); therefore, for these species, the corridors are likely to direct the dispersing of individuals between individual habitat patches in fragmented landscapes (Öckinger & Smith 2008).

For bumblebees, Kreyer *et al.* (2004) showed that potential barriers, such as forests, may not influence the foraging range of two bumblebee species (*B. terrestris* and *B. pascuorum*). Moreover, Cranmer *et al.* (2012) showed that linear landscape elements (i.e., hedgerows) facilitated the movements of bees between habitat patches.

Consequently, the effects of the surrounding landscape are complex. It has been suggested that the relationship between species diversity and the adjacent landscape partly depends on the landscape heterogeneity and quality (Fahrig 2001, Bergman *et al.* 2008) and the life-history traits (e.g., dispersal ability, trophic level, sociality, specialised resource needs) of the species or species groups (Öckinger *et al.* 2010, Jauker *et al.* 2013).

2.3. The threatened specialist butterfly as surrogate species in conservation planning

One widely distributed and endangered specialist species that has received much attention over recent decades and that has been well studied by

several researchers (Konvička & Kuras 1999, Meglécz *et al.* 1999, Luoto *et al.* 2001, Välimäki & Itämies 2003, Meier *et al.* 2005, Gratton *et al.* 2008, Gorbach & Kabanen 2010) in different regions is Clouded Apollo (Lepidoptera, Papilionidae).

Because the ecology and habitat needs of Clouded Apollo are particularly well known, this butterfly qualifies as an indicator of the habitat quality. Furthermore, due to its conspicuous appearance, this butterfly may be categorised as a flagship species.

Flagship species are targeted surrogate species that are successfully used in the conservation of biodiversity. Due to their attractive appearance, they garner sympathy and financial support from the public sector and thereby help conserve the wider biodiversity (Samways 2005).

Indicator species are organisms whose characteristics (e.g., presence/absence, population density) are used to monitor the status of environmental conditions and other species and to identify important areas of biological diversity (Swihart & Moore 2004).

2.3.1. Species description and biology

Clouded Apollo is a butterfly with a wingspan of 50-60 mm. The forewings of the species are whitish with black veins. There are two black dots at the front edge of the forewings, whereas the outer edge of the forewings is transparent. The hind wings of the butterfly are also whitish with some black veins. There is one black dot in the middle of the wing, and this dot is usually hardly perceptible (Figure 1).

The butterfly is a univoltine species with a flight time from the end of May to the middle of June. The larvae of Clouded Apollo are monophagous on the plant genus *Corydalis* (Papaveraceae). In Estonia, the larvae mainly feed on the leaves of fumewort (*Corydalis solida*). However, *C. intermedia* is also found in Estonia, although it is not as widely distributed as *C. solida*. Fumeworts are understory spring ephemeral plants of deciduous forests. Adult butterflies are polyphagous, i.e., they feed on different flowering plants. In Estonia, the nectar sources for adults are *Geranium* spp., *Ranunculus* spp., *Viscaria vulgaris*, *Anchusa officinalis*, *Knautia arvensis*, and *Glechoma hederacea* (Kesküla 1991, Viidalepp 2000). The butterfly overwinters in the egg stage.

Figure 1. The forewings of Clouded Apollo are partly transparent and have two black dots.

2.3.2. Distribution and status

Clouded Apollo exhibits a Palaearctic distribution. The butterfly is found from Spain to central Asia. Over the entire distribution range, the species has discrete populations. Some authors have distinguished subspecies of *P. mnemosyne* (Sulcs & Viidalepp 1974, Meglécz *et al.* 1997).

In Estonia, Clouded Apollo has been occupying three geographically separated areas: west, northeast, and southeast. In accordance with a regional separation, three subspecies have been described: *P. mnemosyne osiliensis* (Bryk 1922) in Saaremaa Island, *P. mnemosyne estonicus* (Viidalepp 2000) in north-eastern Estonia, and *P. mnemosyne viidaleppi* (Kesküla & Luig 1997) in south-eastern Estonia. The first record of *P. mnemosyne* in north-eastern Estonia is from 1878. In 1922, the butterfly was discovered on the island of Saaremaa, and in 1984, it was found in the southern part of Estonia. The Saaremaa's subspecies is most likely extinct today.

The distribution and abundance of the Clouded Apollo butterfly has declined in Northern European regions, such as Finland (Väisänen & Somerma 1985), Sweden (Bergström 2005), Norway (Aagaard & Hansen 1992), and Central Europe (Konvička & Kuras 1999). However, there are a few studies providing evidence that the species increases its abundance and expands its distribution area (Gorbach & Kabanen 2010).

Due to the vulnerability of the populations of Clouded Apollo and due to several reports on local extinctions and/or the limited distribution of populations (Bergström 2005), the species is protected in Europe by the Bern Convention, the EU Habitat Directive (CEE Habitat Directive 43/92, annex IV), and national protection acts and is included in the many regional Red Data Books. In Estonia, the butterfly has been under legal protection since 1995.

2.3.3. Habitat requirements

In general, Clouded Apollo is a butterfly species that depends on early successional biotopes as grassland communities. For example, in Northern Europe, the species occurs in flat semi-natural grasslands (Luoto *et al.* 2001). In Central Europe, the butterfly is found in forest steppes, sparse deciduous forests, and forest clearings (Konvička & Kuras 1999). In Estonia, Clouded Apollo generally occurs in smaller meadow patches adjacent to deciduous forests or bordered by stripes of trees (Meier *et al.* 2005).

In detail, the butterfly needs well-structured habitats due to the different requirements of the larvae and adults (Konvička & Kuras 1999). One factor that determines the suitability of a habitat is the existence of larval food plants. Therefore, the butterfly is generally confined to the conditions required by *Corydalis* species. Luoto *et al.* (2002) and Heikkinen *et al.* (2007) showed that the distribution and occurrence of *P. mnemosyne* in Finland is defined by the cover of deciduous forests. The other factor that makes a biotope suitable for the butterfly is the availability of nectar resources for the adults. High flowering plant species richness is usually found in grassland communities. The effect of semi-natural grassland cover on the occurrence and abundance of Clouded Apollo has been studied by Luoto *et al.* (2001), Välimäki & Itämies (2003), and Heikkinen *et al.* (2007). All of these researchers concluded that the distribution of the species is greatly determined by the cover of semi-natural grasslands. Furthermore, several studies have shown the importance of well-connected habitat patches for the populations of Clouded Apollo (Välimäki & Itämies 2003, Gorbach & Kabanen 2010). The importance of the connectedness of the habitat patches for the butterfly is related to its migration ability and its sensitivity to high wind speeds.

3. AIMS OF THE THESIS

In the conservation of biodiversity, there is a focus on the conservation of a single species or the conservation of specific taxonomic and functional groups within landscapes. To develop more effective conservation strategies, it is essential to obtain detailed knowledge on the responses to environmental factors of a key indicator (e.g., a single species or a single pollinating insect community), which would therefore support a landscape-based conservation (Dover & Settele 2009, Shreeve & Dennis 2011).

A number of studies have shown controversial results on the species richness and abundance of pollinating insects in relation to environmental factors at different spatial scales. There are several potential explanations for the multifarious results, but the main reason lies in the knowledge that insect families, species inside the families, and even the same species respond differently to the habitat characteristics, land-use types, and landscape structures in different regions.

Therefore, various lines of evidence on the relationship between species/communities and environmental factors within different landscape contexts is important for the development of well-designed conservation treatments to maintain or increase pollinating insect populations, particularly in areas where the populations of the species are considered to be in decline.

Specifically, the goals of this thesis were the following:

- To estimate the species richness and abundance of three pollinating insect groups (butterflies, day-active moths and bumblebees) in semi-natural meadows in the north-eastern part of Estonia (Paper I).
- To contribute to a better understanding of the effect of habitat patch characteristics and adjacent landscape structure on the species richness and abundance of target species groups (Papers II and III).
- To provide an overview of the distribution and general habitat requirements of one specialist butterfly species with very complex life cycle and habitat requirements - the threatened butterfly Clouded Apollo in Estonia (Papers IV and V).

4. MATERIAL AND METHODS

The research study on bumblebees, butterflies, and day-active moths was conducted in Ida-Virumaa County. The materials and methods of the study are similar to those used in the thesis of Isabel Diaz Forero (Diaz Forero 2011) because the data were collected and analysed together. However, her thesis focused only on the analysis of bumblebees.

The study of the distributional changes of Clouded Apollo is based on a dataset from all of Estonia.

4.1. Pollinating insect study in Ida-Virumaa

4.1.1. Study region and study sites

Ida-Virumaa County is located in north-eastern Estonia (Figure 2). The region covers an area of 336,400 ha, which accounts for approximately 7.5% of the total area of Estonia. Approximately 58.0% of the territory in the region is covered by forest (coniferous and mixed forests comprised mostly of pines, spruces, and birches). In lesser proportions, the region is covered by arable land (approximately 12.4%), young forest (approximately 6.5%), meadows (approximately 5.7%), and other land cover types (human settlements, mires, bodies of fresh water, etc.).

The abundance and species richness of pollinating insects were determined in 22 semi-natural meadows (Figure 2) that differ in size, shape, vegetation characteristics, and surrounding landscape cover. The areas of the selected meadows ranged from 0.10 to 3.83 with a mean of 1.66 ha. In the northern part of the region, semi-natural meadows are mainly situated in coastal areas, whereas in the central and southern parts, these meadows are mainly found along rivers.

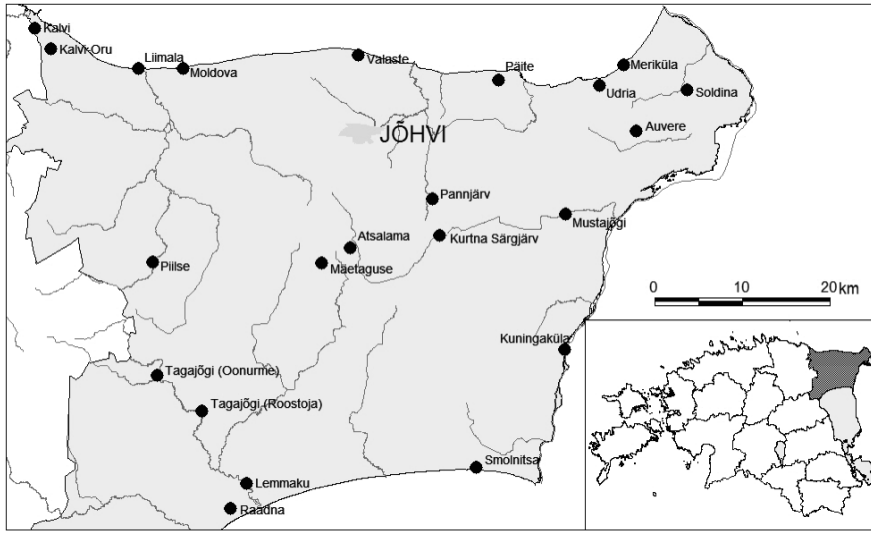

Figure 2. The study region is located in the north-eastern part of Estonia. The locations of the study sites are shown by black dots.

4.1.2. Pollinating insect censuses

We studied pollinating insect communities during the summers of 2008 and 2009. In all study sites, butterflies (Papilionoidea and Hesperioidea), day-active moths (including burnet moths (Zygaenidae, Sphingidae, and Sesiidae), and bumblebees (genus *Bombus*, also including the former subgenus *Psithyrus*) were recorded two times per year, during the period from June to the first half of August.

The insect counts were conducted for approximately 45-60 minutes during each visit using systematic walking surveys (Kumar *et al.* 2009). The pollinating insect sampling took place between 10 a.m. and 4 p.m. on sunny days with little wind. The species and individuals of flower-visiting insects were identified by sight at each meadow. However, the insects that could not be identified at a distance were, when possible, caught by a hand net for later identification in the laboratory. The species of the genus *Leptidea* (*L. sinapis* and *L. reali*) were grouped together. The nomenclature of the studied insect species follows Fauna Europaea (2012).

4.1.3. Patch and landscape characteristics

The habitat patch and landscape characteristics chosen in this thesis could theoretically influence or have influenced pollinating insect species richness and abundance in other studies.

At the patch scale, we determined all of the flowering plant species (SRFFlowPlants), estimated the per cent cover of the plants in the flowering stage (AvCoverFP), and measured the vegetation height (AvGrassH). The per cent cover of flowering plants was determined by visually estimating the overall coverage at each study site. In addition, five indices were calculated at all study sites using Fragstats 3.3: patch area (AREA), perimeter (PERIM), shape index (SHAPE), fractal dimension index (FRAC), and edge density (ED).

At the landscape scale, we calculated the proportion of the primary land cover types in the area surrounding each study site using ArcGIS 9.3. We used a digital 1:10,000 scale Estonian Basic Map provided by the Estonian Land Board. In the study, we considered five different types of land cover: meadows, forests, young forests (including shrubs and young trees), arable land, and human settlements (including residential areas, private areas, buildings, cattle sheds, roads, ruins, and greenhouses). Additionally, five Fragstats indices were calculated: patch richness density (PRD), interspersion and juxtaposition index (IJI), edge density (ED_LAND), Shannon's diversity index (SHDI), and the mean patch area of forest (AREA_MN). All landscape variables were estimated at four spatial scales: radii of 250, 500, 1000, and 2000 m.

4.1.4. Data analysis

Spearman rank order correlations were used to analyse the relationships between total species richness and abundance of butterflies, day-active moths, bumblebees and the patch-scale and landscape-scale variables. The correlation was considered statistically significant if the p value was less than 0.05. Partial least squares (PLS) analysis was performed to simultaneously study the overall butterfly, day-active moth, and bumblebee species richness and abundance and different landscape characteristics. A stepwise forward-selection multiple regression analysis was used to determine the combinations of the most important predictors for total butterfly, day-active moth, and bumblebee species richness and abundance.

For each landscape variable, the spatial scale with the strongest relationship was selected, and a significance level of 0.15 was used instead of the conventional 0.05 because it was the default limit used by the software and because it decreases the chance of omitting potentially significant arguments in the final result during the model building process. For the analysis of correlations and multiple regressions, STATISTICA 9 was used. The PLS analysis was performed using the SAS 9.1 software.

4.2. Data collection and analysis of Clouded Apollo

We organised all of the known records of Clouded Apollo findings in Estonia in a database. The data of the occurrence of the butterfly were derived from various sources, such as the literature, insect collections, records from researchers, and local surveys of the butterfly.

Most of the earlier records were more general, i.e., they described the name of the place or the description of the location using landmark features, such as roads, rivers, trees, and bushes, and some of the data were described within a 10×10 km UTM square. The accuracy of these data was several kilometres (at least 5 km). The records from 1981-2010 were obtained from the national periodical review called LepInfo (a publication of the Estonian Lepidopterologists' Society and the Section for Entomology of the Estonian Naturalists' Society that collects all findings of most butterfly species in Estonia). The accuracy of these records is generally better than that of the older data because all of these records are fixed according to the coordinates of the Estonian national grid system (10×10 km) and the concurrent international UTM grid system. During the last ten years, records of the butterfly (and the exact position of the habitat patch) have been additionally collected using portable GPS units.

All descriptions of the findings of the butterfly were linked from a digital cadastral map of Estonia (1:10,000) to the common GIS database using MapInfo Professional 9.0. The database of Clouded Apollo consists of data on the exact location of the findings (place name or coordinates if possible), accuracy class on a 1-3 scale (1: exact location, 2: grid system coordinates, 3: descriptive location), date and time of the observation, name of the observer, gender, number of individuals (if determined and counted), source of data, and a short description of the habitat.

For the analysis of the distribution changes, we divided our data into five study periods: 1878-1969, 1970-1979, 1980-1989, 1990-1999, and 2000-2010. The first period is longer than the rest because there were only single records of the butterfly from this period.

For the analysis of the relationship between the butterfly occurrence and the general habitat characteristics, we selected the middle part of the River Ahja due to the availability of a detailed habitat description (land use, adjacent land cover type, and dominant plants) and a butterfly survey (occurrence and the number of butterflies) that was conducted in June 2003. In addition, the habitat patch area was drawn in GIS (MapInfo Professional 9.0) to calculate the general patch characteristics (area and perimeter). We defined the habitat patch as a unit of vegetation type (i.e., meadow) that differs in appearance from its surroundings (Forman & Gordon 1986).

5. RESULTS

5.1. Pollinating insects in Ida-Virumaa

5.1.1. Species richness and abundance of butterflies, day-active moths, and bumblebees (Paper I)

A total of 768 individuals of 56 species of butterflies were recorded (Figure 3, the list of species is found in Appendix). The average species richness of butterflies was 15.6. The most abundant butterfly species were *Coenonympha glycerion* (8.5%), *Aphantopus hyperantus* (8.1%), and *Thymelicus lineola* (7.9%). In our study region, we found five species of butterflies that are protected under the EU Habitat Directive: *Parnassius mnemosyne*, *Lycaena dispar*, *Euphydryas maturna*, *Euphydryas aurinia*, and *Coenonympha hero*.

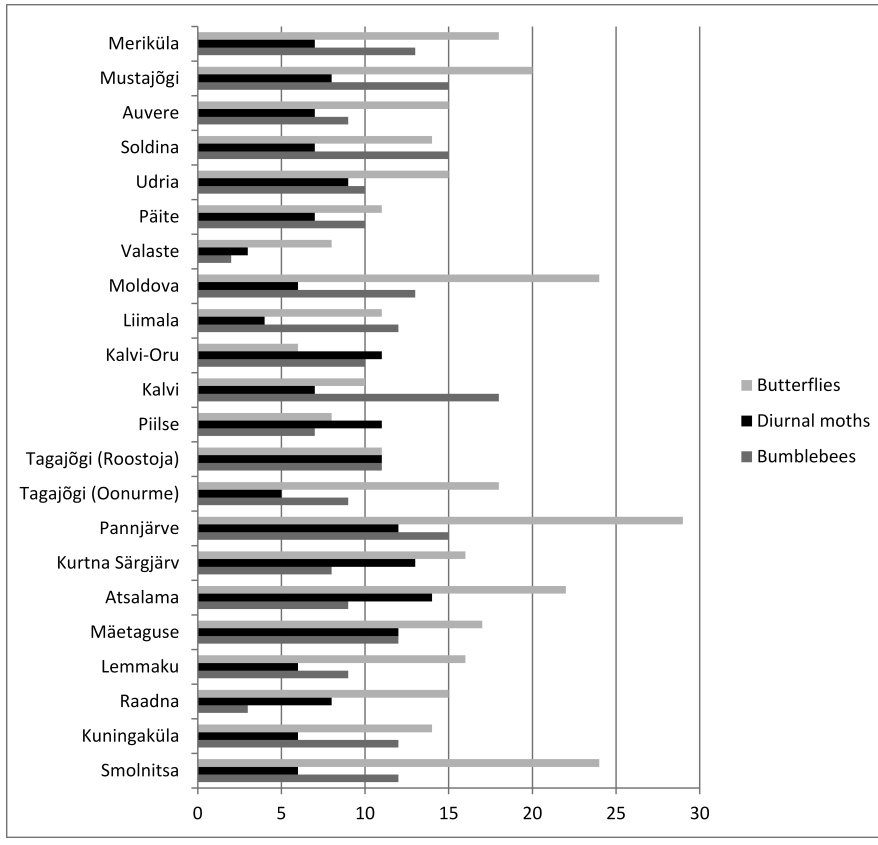

Figure 3. Number of species of pollinating insects in each study site.

A total of 330 individuals of 42 species of day-active moths were recorded (Figure 3, the list of species is found in Appendix). The average species richness of day-active moths was 8.2. The most abundant day-active moth species were *Siona lineata* (14.5%) and *Scopula immorata* (13.6%).

A total of 597 individuals of 24 species of bumblebees (including five species of cuckoo bumblebees) were recorded (Figure 3, the list of species is found in Appendix). An average bumblebee species richness of 10.7 was found per study site. The most abundant species were *B. pascuorum* (23.5%), *B. lucorum* (11.7%), and *B. ruderarius* (9.7%). In the case of cuckoo bumblebees, *B. bohemicus* was the most abundant and accounted for 5.5% of the total number of bumblebee individuals.

5.1.2. Relationships between habitat patch and landscape characteristics and Lepidoptera (Paper II)

At the patch scale, there were no statistically significant relationships between the habitat characteristics and the presence of butterflies and day-active moths.

At the landscape scale, we found that the proportion of forest in the areas surrounding the study sites was positively correlated with the butterfly species richness at 250 m. In contrast, the proportion of meadows in the surrounding landscape at the scales 250, 500, and 1000 m had a significant negative effect on the butterfly species richness and abundance (Table 1).

Concerning the relationships between butterflies and the calculated landscape indices, we found a statistically significant and negative relationship between the interspersion and juxtaposition index and the butterfly species richness at the spatial scale of 500 m. The day-active moth abundance and species richness were both negatively correlated with Shannon's diversity index at 500 and 1000 m (Table 1).

Table 1. Correlations (r_s) between environmental variables and Lepidoptera species richness and abundance.

Variable	Butterflies				Day-active moths			
	abundance		richness		abundance		richness	
	r_s	p	r_s	p	r_s	p	r_s	p
at landscape scale								
PForest R250			0.428	0.047				
PMeadows R250	-0.508	0.015	-0.514	0.013				
PMeadows R500	-0.598	0.003	-0.544	0.008				
PMeadows R1000	-0.512	0.014	-0.427	0.047				
IJI R500			-0.458	0.032				
SHDI R500					-0.481	0.022	-0.469	0.027
SHDI R1000					-0.547	0.007	-0.447	0.036

5.1.3. Relationship between habitat patch and landscape characteristics and bumblebees (Paper III)

At the patch scale, we found three statistically significant correlations between bumblebees and habitat characteristics. The bumblebee abundance was positively associated with the flowering plant species richness. The bumblebee species richness was negatively correlated with the shape index and negatively correlated with the fractal dimension index (Table 2).

At the landscape scale, we found ten statistically significant correlations between bumblebees and landscape characteristics (Table 2). The bumblebee species richness was negatively associated with the proportion of forest at the spatial scales of 1000 m and 2000 m. Similarly, the species richness was negatively correlated with the proportion of young forest at the spatial scales of 250 m and 500 m. In addition, the bumblebee species richness responded negatively to the mean patch area of forest at the spatial scale of 2000 m. In contrast, the species richness was positively correlated with the proportion of meadows at the largest spatial scale, i.e., 2000 m. The proportion of human settlements was positively correlated with bumblebee abundance at 250 m and 1000 m, and the bumblebee abundance was positively associated with Shannon's diversity index at the spatial scale of 2000 m and the edge density at 1000 m (Table 2).

Table 2. Correlations (r_s) between environmental variables and bumblebee species richness and abundance.

Variable	Bumblebees			
	abundance		richness	
	r_s	p	r_s	p
at patch scale				
SRFFlowPlants	0.65	<0.001		
SHAPE			-0.60	0.003
FRAC			-0.57	0.004
at landscape scale				
PForest R1000			-0.45	0.036
PForest R2000			-0.47	0.025
Pbrushw R250			-0.57	0.005
Pbrushw R500			-0.44	0.040
PMeadows R2000			0.51	0.015
PHumSet R250	0.48	0.024		
PHumSet R1000	0.51	0.014		
ED_LAND R1000	0.50	0.018		
SHDI R2000	0.44	0.039		
AREA_MN R2000			-0.51	0.015

5.1.4. Connectivity patterns between pollinating insects and various factors at the patch and landscape scales (Papers II and III)

5.1.4.1. Butterfly species richness and abundance

Two connectivity patterns were identified using partial least squares analysis, which together accounted for 100% of butterfly richness and abundance variance and 26% of patch and landscape characteristics variance (in Figure 4, the percentages are presented separately for the two connectivity patterns).

The first connectivity pattern connects the overall number of butterfly species and individuals with the patch and landscape characteristics (first singular vector, Figure 4). The overall butterfly richness and abundance were negatively correlated with the proportion of meadows at all spatial scales and with the proportion of arable land at the 250 and 500 m spatial scales.

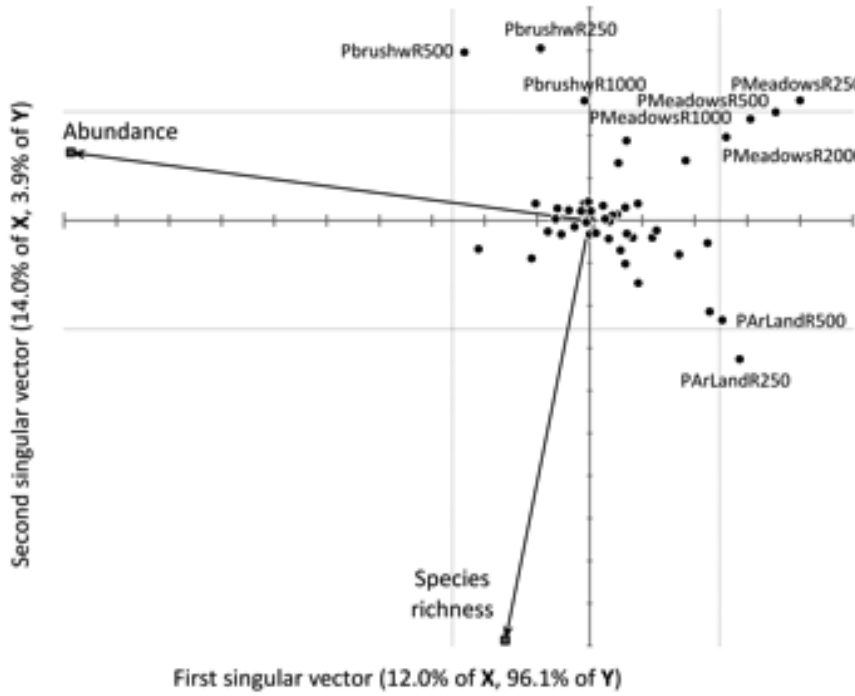

Figure 4. Results of the partial least squares correlation analysis (PLS) of butterflies. Dots mark the location of patch and landscape characteristics (**X**), and squares with arrows mark the location of the butterfly adjusted richness and abundance (**Y**) in relation to the two latent factors. The patch and landscape characteristics with $p < 0.1$ (as assessed through permutation tests) are presented with the corresponding variable name. R250, R500, R1000 and R2000 denote the different spatial scales at which the landscape factors were calculated.

The second connectivity pattern (second singular vector, Figure 4) reflects the changes in relative butterfly species richness (i.e., the heterogeneity or homogeneity of the study sites in relation to the number of individuals) and its relation with the patch and landscape factors. Negative correlations were only found for the second singular vector values corresponding to the proportion of young forest (brushwood) at the spatial scales of 250, 500 and 1000 m. Butterfly species richness may be relatively higher (compared with the number of individuals) if the proportion of young forest is low (especially at the smallest spatial scale) in the surrounding area of the semi-natural meadow patch.

5.1.4.2. Day-active moth species richness and abundance

Two connectivity patterns were identified using partial least squares analysis, and together, these accounted for 100% of the day-active moth richness and abundance variance and 16.8% of the patch and landscape characteristics variance (in Figure 5, the percentages are presented separately for the two connectivity patterns).

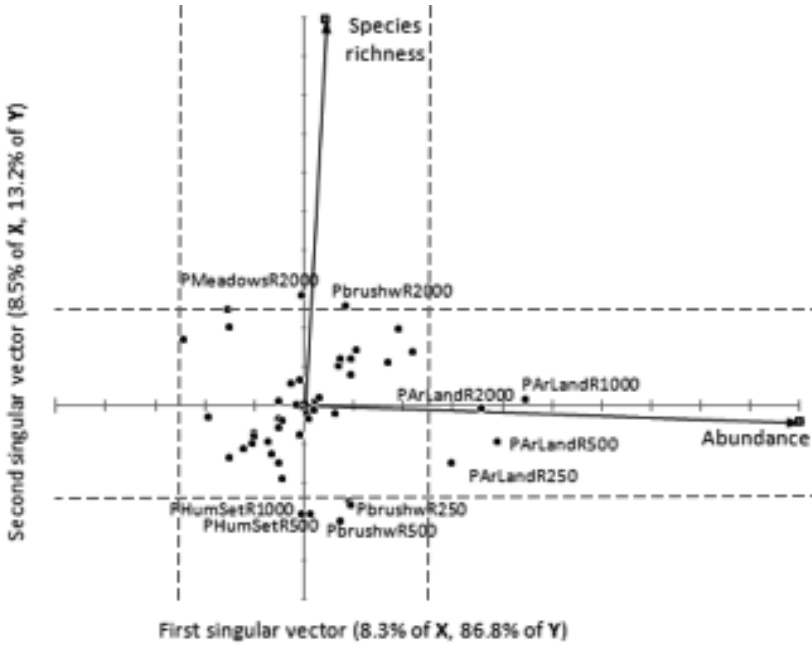

Figure 5. Results of the partial least squares correlation analysis (PLS) for day-active moths. The dots mark the location of the patch and landscape characteristics (**X**), and the squares with arrows mark the location of the day-active moth adjusted richness and abundance (**Y**) in relation to the two latent factors. The patch and landscape characteristics with $p < 0.1$ (as assessed through permutation tests) are presented with the corresponding variable name. R250, R500, R1000 and R2000 denote the different spatial scales at which the landscape factors were calculated.

The first connectivity pattern connects the overall number of day-active moth species and individuals with the patch and landscape characteristics (first singular vector, Figure 5). The overall moth richness and abundance were positively correlated with the proportion of arable land at all spatial scales.

The second connectivity pattern (second singular vector, Figure 5) reflects the changes in the relative day-active moth species richness (i.e., how

heterogeneity or homogeneity of the study sites in relation to the number of individuals) and its relation with the patch and landscape factors. Positive correlations were only found for the second singular vector values corresponding to the proportion of meadows at the spatial scale of 2000 m and the proportion of young forest (brushwood) at 2000 m. The negative second singular vector values of the proportion of human settlements at the spatial scales of 500 and 1000 m and the proportion of young forest at the spatial scales of 250 and 500 m indicate that the relative species richness may be lower (compared with the number of individuals) if the proportions of human settlement and brushwood is high in the surrounding area of the semi-natural meadow patch.

5.1.4.3. Bumblebee species richness and abundance

Two connectivity patterns were identified with partial least squares analysis, and these two patterns together accounted for 100% of the bumblebee richness and abundance variance and 31.5% of the patch and landscape characteristics variance (in Figure 6, the percentages are presented separately for the two connectivity patterns).

The first connectivity pattern connects the overall number of bumblebee species and individuals with the patch and landscape characteristics (first singular vector, Figure 6). The overall bumblebee richness and abundance were positively correlated with the proportion of human settlements at the smallest spatial scale. In contrast, the proportion of arable land at the scale of 250 m and the mean patch area of forests at larger spatial scales were negatively related with the overall bumblebee richness and abundance pattern.

The second connectivity pattern (second singular vector, Figure 6) reflects the changes in the relative bumblebee species richness (i.e., how heterogeneity or homogeneity of the study sites in relation to the number of individuals) and its relation to the patch and landscape factors. Positive correlations were only found for the second singular vector values corresponding to the proportion of arable land at the spatial scale of 2000 m and the proportion of meadows at 2000 m. The negative second singular vector value was the proportion of human settlements at the spatial scale of 500. This relationship indicates that the relative bumblebee species richness may be lower (compared with the number of individuals) in landscapes where the proportion of human settlements are high.

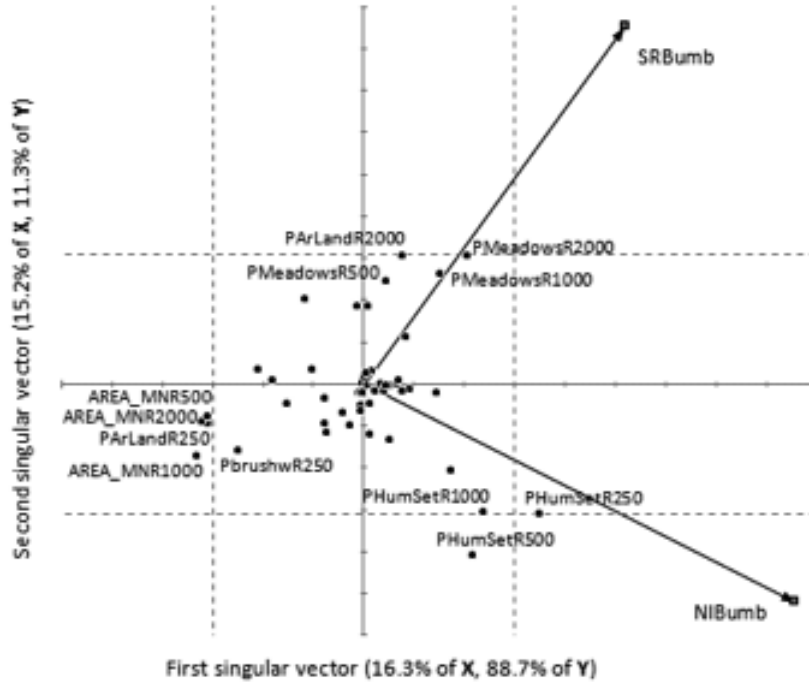

Figure 6. Results of the partial least squares correlation analysis (PLS) for bumblebees. The dots mark the location of the patch and landscape characteristics (**X**), and the squares with arrows mark the location of the bumblebee adjusted richness and abundance (**Y**) in relation to the two latent factors. The patch and landscape characteristics with $p < 0.1$ (as assessed through permutation tests) are presented with the corresponding variable name. R250, R500, R1000 and R2000 denote the different spatial scales at which the landscape factors were calculated.

5.1.5. Models for the prediction of the richness and abundance of pollinating insect species (Papers II and III)

5.1.5.1. Butterflies

The regression models based on the patch and landscape factors tested explained 68% of the variation in total butterfly abundance and 29% of the species richness.

The model for total butterfly abundance included five variables: two patch-scale factors and three landscape-scale factors (Table 3). Species richness of flowering plants was significantly positively related with butterfly abundance and emerged as the most important predictor in

the model. All other variables (average cover of flowering plants, patch richness density at the 250 m spatial scale, proportion of meadows and interspersion and juxtaposition index at 500 m) were negatively correlated with total butterfly abundance.

Table 3. Multiple regression models for total butterfly abundance and species richness (adjusted to the common number of individuals).

Dependent variable	R^2 (p-value)	Variable included in the model	Regression coefficient	p-value
Total butterfly abundance	0.68 (0.002)	Species richness of flowering plants (SRFlowPlants)	1.61	<0.001
		Average percent cover of flowering plants (AvCoverFP)	-0.38	0.008
		Proportion of meadows at 500 m (PMeadows R500)	-0.33	0.135
		Patch richness density at 250 m (PRD R250)	-0.39	0.084
		Interspersion and juxtaposition index at 500 m (IJI R500)	-1.21	0.005
Total butterfly species richness (adjusted)	0.29 (0.010)	Proportion of meadows at 500 m (PMeadows R500)	-0.04	0.010

The model for total butterfly species richness included only one landscape-scale factor (Table 3). Adding other variables did not significantly improve the model. The proportion of meadows in the surrounding landscape at the 500 m spatial scale was negatively correlated with total butterfly species richness.

5.1.5.2. Day-active moths

The regression models constructed based on the patch and landscape factors tested explained 70% of the variation in the total day-active moth abundance and 71% of the species richness.

The model for total moth abundance included five variables: two patch-scale factors and three landscape-scale factors (Table 4). The most important predictor of moth abundance was Shannon's diversity index at the spatial scale of 500 m, which was significantly and negatively

Table 4. Multiple regression models for total day-active moth abundance and species richness (adjusted to the common number of individuals).

Dependent variable	R^2 (p-value)	Variable included in the model	Regression coefficient	p-value
Total day-active moth abundance	0.70 (<0.001)	Edge density (ED)	-0.01	0.003
		Species richness of flowering plants (SRFlowPlants)	0.49	0.013
		Interspersion and juxtaposition index at 500 m (IJI R500)	0.46	0.029
		Proportion of arable land at 250 m (PArLand R250)	0.15	0.030
		Shannon's diversity index at 500 m (SHDI R500)	-23.21	<0.001
Total day-active moth species richness (adjusted)	0.71 (0.002)	Average vegetation height (AvGrassH)	0.02	0.010
		Proportion of young forest at 500 m (Pbrushw R500)	-0.09	0.039
		Patch richness density at 2000 m (PRD R2000)	-3.64	0.004
		Interspersion and juxtaposition index at 250 m (IJI R250)	-0.04	0.037
		Shannon's diversity index at 1000 m (SHDI R1000)	-1.98	0.026
		Mean patch area of forest at 250 m (AREA_MN R250)	-0.17	0.026

correlated with moth abundance. The species richness of flowering plants, the interspersion and juxtaposition index at the spatial scale of 500 m, and the proportion of arable land at 250 m were all positively related with moth abundance, whereas the edge density was negatively associated with total moth abundance.

Six variables were included in the model for total moth species richness: one patch-scale factor and five landscape-scale factors (Table 4). The average grass height was positively related with moth richness, whereas all landscape-scale factors were negatively correlated with the dependent variable. The most important predictor of total moth species richness was the patch richness density at the 2000 m spatial scale.

5.1.5.3. Bumblebees

The regression models constructed based on the patch and landscape factors tested explained 83% of the variation in total bumblebee abundance and 73% of the species richness (Table 5).

The total bumblebee abundance was best described by a model containing four variables: one patch-scale factor and three landscape-scale factors (Table 5). The most important predictor of bumblebee abundance was the species richness of flowering plants, which was significantly and positively correlated with the abundance of bumblebees. All three landscape variables (the proportion of arable land at the smallest spatial scale, the mean patch area of forest and the edge density, both at 1000 m) were negatively correlated with bumblebee abundance.

The species richness of bumblebees was best described by a model containing five variables: two patch-scale factors and three landscape-scale factors (Table 5). The most important predictor of bumblebee species richness was the shape index, which showed a negative relationship. The patch area was positively correlated with bumblebee species richness. All of the three landscape variables (the proportion of arable land at the largest spatial scale, the mean patch area of forest at 1000 m, and the patch richness density at the 500 m spatial scale) were negatively related with bumblebee species richness.

Table 5. Multiple regression models for total bumblebee abundance and species richness (adjusted to common number of individuals).

Dependent variable	R^2 (p-value)	Variables included in the model	Regression coefficient	p-value
Total bumblebee abundance	0.83 (<0.001)	Species richness of flowering plants (SRFlowPlants)	0.44	<0.001
		Proportion of arable land at 250 m (PArLand R250)	-0.08	0.008
		Mean patch area of forest at 1000 m (AREA_MN R1000)	-0.12	0.048
		Edge density at landscape level (ED_LAND)	0.09	0.120
Total bumblebee species richness (adjusted)	0.73 (<0.001)	Patch area (AREA)	0.18	0.028
		Shape index (SHAPE)	-0.88	0.003
		Proportion of arable land at 2000 m (PArLand R2000)	-0.05	0.025
		Mean patch area of forest at 1000 m (AREA_MN R1000)	-0.16	<0.001
		Patch richness density at 500 m (PRD R500)	-0.13	0.103

5.2. Study of Clouded Apollo

5.2.1. Distribution of the butterfly in Estonia (Paper IV)

There are 307 records of Clouded Apollo in Estonia from the period 1878-2010. Of the five study periods, most distribution records (82%) are from 1980 and later. Only 18% of all records are from the period 1878-1979.

During the first study period (1878-1969), there are 41 records of Clouded Apollo, and the majority of these are located in eight places in north-eastern Estonia and only one location (Kübassaare) on the island of Saaremaa (Table 6). During the period 1970-1979, there are 13 records of the butterfly; the majority of these are located in north-eastern Estonia, and one is found on the island of Saaremaa. During these two study periods, the number of individuals of Clouded Apollo observed at the sites of findings varied between 1 and 44. During the period 1980-1989, there are 32 records of Clouded Apollo in Estonia. The butterfly was registered 19 times in north-eastern Estonia and 13 times in south-eastern

Estonia. The number of individuals varied from 1 to 37. During the periods 1990-1999 and 2000-2010, there are 95 and 126 records of the butterfly, respectively. Approximately two thirds of the findings from the last two study periods are located in south-eastern Estonia, where the number of recorded individuals has reached 300.

Table 6. Summary of records of Clouded Apollo in Estonia.

Study periods	Regions	No. of findings per region	No. of sites per region	No. of individuals per site
1878-1969	NE	32	8	1-44
	W	9	1	1-20
	SE	-	-	-
1970-1979	NE	12	6	1-17
	W	1	1	-
	SE	-	-	-
1980-1989	NE	19	11	1-37
	W	-	-	-
	SE	13	9	1-9
1990-1999	NE	14	11	1-50
	W	-	-	-
	SE	81	42	1-200
2000-2010	NE	57	48	1-60
	W	-	-	-
	SE	69	44	1-300

The changes in the distribution trends of Clouded Apollo in Estonia are shown in Figure 7. During the period 1878-1969, the distribution of the butterfly remained local in north-eastern Estonia. During the periods 1970-1979 and 1980-1989, the species moved westward with decennial maximum expansion distances of approximately 30 km and 20 km, respectively (Figure 7). During the last two decades (1990-1999 and 2000-2010), the expansion of the butterfly has continued to the west and to the south. In contrast, on the island of Saaremaa, the butterfly was found during the period 1922-1973, but it remained local and few in number in this habitat throughout the study period.

Until the middle of the 1980s, Clouded Apollo was found only in north-eastern Estonia and on the island of Saaremaa. In southern Estonia, the butterfly was first recorded in 1984 near the rivers Pedetsi and Piusa. The butterfly was then found approximately 40 kilometres to the north in the

Ahja River catchment six years later and approximately 35 kilometres to the northwest in the Võhandu River catchment five years later. A more substantial increase (30 to 50 km) in occupancy to the north and north-westerly directions was observed in the period 1990-2000.

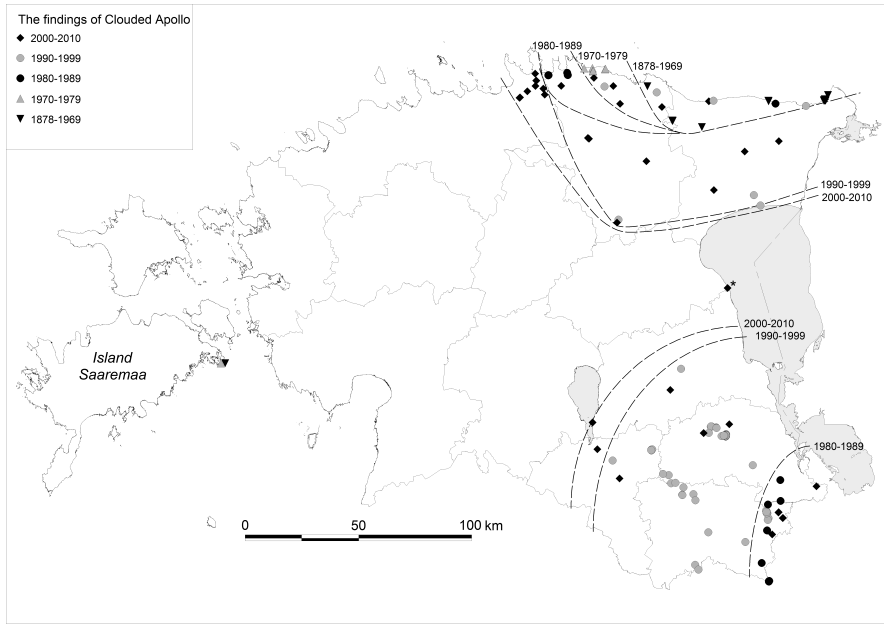

Figure 7. Distribution of Clouded Apollo in Estonia in 1878-2010. The broken lines show the extent of the butterfly distribution in a given period. The record with an asterisk (*) concerns a single instance from the year 2002 (five individuals) with no later records at that site. Therefore, the 2000-2010 line was not drawn to include this record.

5.2.2. Habitat preferences of the butterfly (Paper V)

In the middle part of the River Ahja, we digitised 17 meadow patches occupied by Clouded Apollo. The habitat patches varied from 0.73 to 4.71 (mean=2.24) ha in size. The perimeters of the habitat patches were between 405.3 to 1431 m (mean=775.5 m). The occupied habitat patches are situated along the banks of the river, and at least one side is surrounded by forest. Furthermore, the study also showed that the butterfly was mainly related to dry meadow with a riparian strip of bushes and trees, particularly grey alder (*Alnus incana*) (Figure 8). The abundance of the butterfly was as high as 200 individuals per hectare in four meadows; however, in most cases, the abundance was between 11 and 51 individuals.

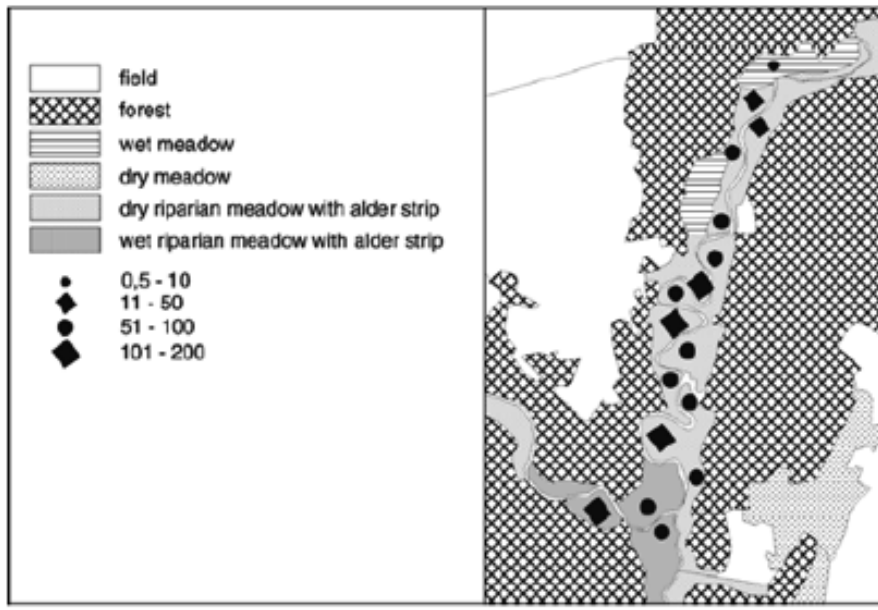

Figure 8. Habitat type structure and density (individuals per hectare) of Clouded Apollo in the Ahja River valley in south Estonia.

6. DISCUSSION

In this study, our results showed that the habitat patch characteristics and surrounding landscape composition and configuration are important for pollinating insect communities. Moreover, the studied insect groups responded different to the habitat and landscape compositions. The taxon-specific reaction to habitat and surrounding landscape factors has been shown by many recent studies (e.g., Sjödin *et al.* 2008, Ekroos *et al.* 2010, Öckinger *et al.* 2012). Different responses are related to ecological differences between species and groups (Öckinger *et al.* 2010, Jauker *et al.* 2013).

6.1. Effects of patch-scale factors on pollinating insects

We found that the plant species richness had a positive effect on the abundance of the investigated pollinating insects. These results are consistent with previous studies on butterflies, day-active moths (Bergman *et al.* 2008, Marini *et al.* 2009), and bumblebees (Pywell *et al.* 2005, Rundlöf *et al.* 2008, Potts *et al.* 2010). This positive association is related to the facts that plant species serve as important food plants for larvae and that flowers provide nectar resources for butterflies and moths and nectar and pollen for bumblebees. Hence, a high plant species richness may be more likely to suffice the host, food, and forage plant requirements, as well as the nesting, mating, and hibernation site requirements, of different flower-visiting insect species (Kumar *et al.* 2009).

In contrast, we found no significant effect of the species richness of flowering plants on the species richness of the studied insect groups. In addition, the proportion of area covered by plants in the flowering stage had also no significant effect on the species richness or abundance of pollinating insects. Various factors may be responsible for this relationship. Bumblebees and many butterfly species are considered to be quite mobile organisms; they usually do not only forage in the patch and, therefore, the floral abundance of the habitat patch is not as important a factor in determining the overall insect species richness and abundance in certain areas. Another possible explanation for butterfly diversity and abundance is that their values may be more influenced by the number and abundance of host plants than the total flower abundance (Sjödin *et*

al. 2008, Krämer *et al.* 2012). A study by Kleijn & Van Langevelde (2006) demonstrated that the bee species richness shows a stronger positive response to the flower abundance in areas with little semi-natural habitats than in areas with more semi-natural habitats.

In the studied landscapes, the vegetation height had no significant effect on the flower-visiting insect species richness and abundance. Similarly, many previous studies have reported that the vegetation height has no significant effects on the species richness or abundance of butterflies and bumblebees (Sjödin *et al.* 2008).

However, both positive and negative relationships between the diversity of concerned flower-visiting insects and vegetation height have also been reported (e.g., Öckinger & Smith 2006, Kumar *et al.* 2009, Winfree *et al.* 2009). Possible explanations for the opposite responses by bees and butterflies may depend on different life-history traits (e.g., dispersal ability, resource requirements, perception of the habitat, and foraging ranges) and the range variation in the vegetation height used in the different study areas (Kumar *et al.* 2009).

There were no clear relationships between the different calculated habitat patch characteristics and the species richness and abundance of butterflies and day-active moths. For bumblebees, the species richness was negatively correlated with the shape index and the fractal dimension index. Both indexes describe the complexity of the patch shape. A more irregular habitat shape would decrease the species richness of bumblebees. Hence, habitat patches with a higher core area appear to have a positive influence on bumblebees. A possible explanation is that patches with an increased interior area may have certain conditions or resources (e.g., nesting sites) that bumblebees require.

6.2. Effects of landscape composition on pollinating insects

6.2.1. Proportion of forests

The influence of the proportion of forest in the surrounding landscape on the concerned insect groups showed contrasting results. The species richness of butterflies was significantly positively correlated with the proportion of forest at the smallest (radius 250 m) landscape scale,

whereas the forest cover in the surrounding landscape had no effect on the day-active moth species richness and abundance. Contrary to butterflies, the bumblebee species richness was negatively influenced by the presence of young forest in the surrounding landscape at the smallest spatial scales and by the presence of forest at the largest spatial scales.

The importance of a forest habitat for butterflies is consistent with previous investigations (Kuussaari *et al.* 2007; Bergman *et al.* 2008; Marini *et al.* 2009, Krämer *et al.* 2012). In the study conducted by Marini *et al.* (2009), the proportion of woody vegetation had the strongest effect on the butterfly species richness at the local spatial scale. The significance of the forest disappeared with an increase in the spatial extent.

There are several potential explanations for the butterfly species' positive response to a forest habitat located in the immediate vicinity of their semi-natural habitat patch. First, edge habitats are influenced by environmental conditions characteristic of the adjacent communities and are thereby different from the interior habitats. For example, forest edges exhibit significant gradients of solar radiation, temperature, wind speed, and moisture (humidity) between the forest interior and the adjacent meadow habitat. As a result of their diverse microclimate and compositional structure, forest edges may provide complementary resources, such as nectar plants for adults and host plants for larvae. Additionally, certain structures may provide suitable sites for female oviposition and for the immature stage to accomplish their life cycle (Ouin *et al.* 2004). Several studies have shown that many butterfly species evade open areas, such as the habitat patch interior due to the increase wind speed, but woody vegetation offers shelter against the wind (Kuussaari *et al.* 2007, Kumar *et al.* 2009, Rosin *et al.* 2012). Furthermore, a forest habitat in the close vicinity can serve as refuge for insects when grasslands are disturbed (Debinski *et al.* 2001, Ouin & Burel 2002, Marini *et al.* 2009). Because butterfly assemblages consist of species with different habitat requirements, the increased edge density benefits species that require mixed cover types. Linear elements in the landscape also have a positive effect on butterfly diversity (Saarinen *et al.* 2005, Sjödin *et al.* 2008).

The negative effect of the surrounding forest cover on the bumblebee species richness is difficult to explain because it has been suggested that

deciduous forests or forest edges (e.g., willows) can provide additional forage resources for less specialised species (e.g., early emerging bumblebee species) (Goulson *et al.* 2005). Furthermore, Kreyer *et al.* (2004) showed that potential barriers, such as forests, may not influence the foraging range of two bumblebee species (*B. terrestris* and *B. pascuorum*). However, it is possible that some bumblebee species may not be able to find suitable nesting sites in the forest or near forest edges (Goulson 2010) and may also differ in the foraging and passing of forest strategies (Kreyer *et al.* 2004, Diekötter *et al.* 2006). In contrast, in our study region, the forests are conifer-dominated and therefore may lack the key resources that bumblebee species need for survival.

6.2.2. Proportion of meadows

In contrast to our expectations, we found that the total butterfly species richness was significantly negatively associated with the proportion of meadow at the spatial scales of 250 m, 500 m, and 1000 m. Similarly, the abundance of butterflies was negatively associated with meadow coverage. Furthermore, the model for predicting the total butterfly species richness consisted of a single variable, namely the proportion of meadow at 500 m, which was negatively correlated with the butterfly species richness. A likely reason for the negative association between the proportion of meadow habitat and the butterfly species richness and abundance at the local landscape scale is that a higher amount of meadows, which are open habitats, increase the overall openness of the landscape. The negative influence of wind on butterfly behaviour has been previously reported (e.g., Dover *et al.* 1997). In addition, the observed negative effect of an increase in the landscape openness is also in accordance with our results, as indicated by the positive effect of an adjacent forest habitat on the butterfly species richness and abundance. Recent studies have provided increasing evidence that butterflies prefer sheltered habitats to open habitats (Pywell *et al.* 2004, Kuussaari *et al.* 2007, Kumar *et al.* 2009, Krämer *et al.* 2012, Rosin *et al.* 2012, Öckinger *et al.* 2012).

For bumblebees, we found that the species richness may increase with an increase in the presence of meadows in the landscape. This relationship is consistent with the results of earlier studies that reported positive relationships between bumblebee communities and the proportion of meadows in the surrounding landscape (Hatfield & LeBuhn 2007, Le Féon *et al.* 2010). This positive association is related to the fact that

meadows provide better-quality habitats and contain relatively higher plant species diversity to support viable populations of bumblebees and other pollinating insects.

6.2.3. Proportion of arable land and human settlements

The relationships between the total species richness, abundance of butterfly species and the proportion of human-influenced land cover types, such as arable land and human settlements were not statistically significant at any of the landscape scales studied. Our results certainly do not assert that anthropogenically influenced land cover types do not influence the total butterfly species richness and abundance. Several studies have shown the negative effects of intensified agricultural areas on butterfly diversity (Flynn *et al.* 2009; Ekroos *et al.* 2010, Ökinger *et al.* 2012). However, Ekroos *et al.* (2010) found a threshold value (60%) above which arable land cover had a stronger negative effect on butterfly diversity. In our study sites, the arable land cover at the largest landscape scale (2000 m) was between 1% and 47%, which may explain why we did not find any significant relationships.

In contrast, some studies have indicated that extensive agriculture enhances the populations of flower-visiting insects (Weibull & Östman 2003, Potts *et al.* 2009, Jonason *et al.* 2012). A likely mechanism is that extensive management increases habitat quality for flower-visiting insects, e.g., by increasing nectar availability. Moreover, it has been found that the abundance of highly mobile (generalist) butterfly species in landscapes dominated by arable land is higher (Jonason *et al.* 2012).

For bumblebees, we found that the species richness and abundance were negatively associated with the proportion of arable land. This pattern is supported by previous studies that reported negative relationships between bee species richness and abundance and the proportion of agricultural land in the surrounding landscape (Le Féon *et al.* 2007). This negative association may be related to the fact that agricultural land may provide less foraging and nesting resources for bumblebees (Goulson *et al.* 2005). Furthermore, the foraging resources in arable land are usually temporary and may momentarily facilitate bumblebee survival. In contrast, semi-natural grasslands may provide multifarious and stable resources that are necessary for the long-term survival of bumblebee species (Öckinger & Smith 2007, Jauker *et al.* 2009).

In contrast, we found that the day-active moth species richness and abundance were positively influenced by the proportion of arable land cover at various spatial scales. The positive effect of arable land on moths is difficult to explain because it contradicts the effect of an increase in the landscape openness, which has a negative influence to butterflies by increasing the wind factor. Furthermore, it has been suggested that geometrid moths (majority of the species of day-active moths in our study sites) exhibit a lower average mobility than butterflies (Ekroos *et al.* 2010). Therefore they may be more sensitive to an increase in the landscape openness. However, in our study region, the management of agricultural land is extensive rather than intensive, which allows us to suggest that arable land may provide certain resources valuable for daytime flying moths.

We found no evidence that the percentage of human settlements, such as residential areas, private areas, buildings, cattle sheds, roads, and ruins, is related to butterfly and day-active moth species richness and abundance. Collinge *et al.* (2003) also showed that the percentage of urbanisation in the surrounding landscape does not significantly predict the butterfly species richness in their study area. However, it has been suggested and even declared that some human-influenced land cover types hold and support a high diversity of butterflies and other pollinating insects (Saarinen *et al.* 2005; Noordijk *et al.* 2009).

In the case of bumblebees, we found that the total bumblebee species richness and abundance were positively influenced by the proportion of human settlements at various landscape scales. A likely reason for this positive association is that human settlements, in terms of flower-rich gardens or roadside verges, in the surrounding landscape may enhance the species richness and abundance of flower-visiting insects (Saarinen *et al.* 2005, Noordijk *et al.* 2009, Goulson *et al.* 2010). For example, Goulson *et al.* 2010 found that gardens, in terms of nesting sites, support high densities of bumblebees.

6.3. Effects of landscape configuration on pollinating insects

We found that the butterfly species richness was negatively influenced by the interspersion and juxtaposition index (IJI) at the 500 m spatial scale. Low values of this index characterise landscapes in which patch

types are distributed disproportionally or clumped together, and a greater complexity of landscape is reflected in an increase in the index (Eiden *et al.* 2000). Additionally, we found that Shannon's diversity index appears to be an important landscape metric for day-active moth species richness and abundance at the spatial scales of 500 m and 1000 m. This index also indicates the complexity of the surrounding landscape matrix and increases as the number of different patch types increases and as the distribution of patch types becomes more equitable (Eiden *et al.* 2000). In our study area, the index was negatively related with moth species richness and abundance. Because both indices show the complexity (heterogeneity) of the surrounding habitat and are negatively related with the species richness and abundance of butterflies and moths, we can conclude that moths and butterflies appear to prefer more simplified rather than complex landscapes at the local scale. A possible explanation for this association may be that the studied moth and butterfly communities consist of species that are specialised to forest-grassland habitats and ecotones and therefore mostly depend on the configuration of these land cover types at the local scale.

Contrary to butterflies and day-active moths, the bumblebee species appear to prefer a diverse landscape matrix, particularly at the largest spatial scales, where we found a positive relationship between bumblebee abundance and both the edge density and Shannon's diversity index. A more complex (heterogeneous) landscape matrix may provide diverse resources (e.g., additional forage plants, nesting sites, and refuge sites) for bumblebees and thereby increases their survival possibilities. Furthermore, there is evidence that the foraging distances of some bumblebee species (*B. terrestris* and *B. lapidarius*) range up to approximately 2.5-3 km (Kreyer *et al.* 2004, Westphal *et al.* 2006, Hagen *et al.* 2011). Hence, the larger foraging distances of some species allow the more effective use of food resources in spatially isolated patches.

6.4. Clouded Apollo

The results of the Clouded Apollo study showed that the specialist species has increased its abundance and distribution in Estonia. Over the last 30 years, the abundance and distribution area of the butterfly has increased. The general trend for most European grassland butterflies and the trend in other places for *P. mnemosyne*, are characterised by declines in both

abundance and distribution area (Kuussaari *et al.* 2007, Settele *et al.* 2008). Habitat loss, deterioration of habitat quality, increasing fragmentation of habitat patches, or the combined effects of all of these factors are the main threats to Clouded Apollo (Meglécz *et al.* 1999, Luoto *et al.* 2001, Bergström 2005). In Estonia, the extinction of the subspecies found on Saaremaa Island is most likely related to habitat degradation in particular locations and a lack of other suitable habitats in the vicinity. Therefore, a possible explanation of the pattern of contrasting trends found for Clouded Apollo in different geographical regions is the availability and quality of suitable habitats.

Similarly to other European countries, the traditional extensive agricultural practice is decreasing in Estonia (Kukk & Sammul 2006). However, the area of specific semi-natural grasslands that are suitable habitats for Clouded Apollo remains high. Therefore, the increasing occupancy trend of Clouded Apollo observed in recent decades is likely associated with the fact that the availability of semi-natural grasslands suitable for the butterfly continues to be good.

The study in the middle part of the River Ahja showed that Clouded Apollo prefers quite small semi-natural grassland patches surrounded by a forest on one or more sides. The importance of deciduous forests and semi-natural grassland cover on the occurrence of Clouded Apollo is consistent with previous investigations (Luoto *et al.* 2001, Välimäki & Itämies 2003, Heikkinen *et al.* 2007, Gorbach & Kabanen 2010). This finding is mostly due to the species' habitat requirements. The immature stage develops on forest floor plants but requires warmer microclimate conditions that are not available under closed canopy, and the adults avoid closed canopy conditions but require nectar plant-rich open meadows protected from the wind.

Furthermore, the patterns of occupied habitat patches in Estonia indicate that the Clouded Apollo butterfly is closely related to riverside landscape elements. River valleys provide suitable biotope patterns for the butterfly. The settlement of semi-natural grassland patches in river systems forms corridors and stepping stones that may facilitate butterfly movement (Sutcliffe & Thomas 1996, Haddad 1999, Townsend & Levey 2005). Several studies have confirmed the importance of well-connected habitat patches for the populations of Clouded Apollo (Välimäki & Itämies 2003, Gorbach & Kabanen 2010).

In contrast, the size of the habitat patch and the preference for adjacent woody vegetation is closely related to the threats to the Clouded Apollo butterfly. These relatively small grassland habitat patches tend to fall out of traditional management regimes (e.g., mowing) and pass the processes of natural afforestation, which result in a decrease in the quality of habitat patches and will lead to the extinction of these butterfly populations.

7. CONCLUSIONS

This thesis showed that the habitat patch characteristics (i.e., quality and size of habitat) and surrounding landscape composition (e.g., proportion of meadows and forests) and configuration (heterogeneity) at a spatial scale of up to 2 km are important for pollinating insect communities. Furthermore, butterflies, day-active moths, and bumblebees responded differently to different habitat and landscape factors. Thus, understanding the factors that determine the habitat quality and suitable landscape structure for the species richness, abundance, and community composition of pollinating insects (key indicators) is significant for the assurance of long-term persistence and efficient conservation of these insects and other related taxa (e.g., plants, birds, and other insect groups). Additionally, to mitigate the biodiversity loss of flower-visiting insects, there is a need to increase our knowledge of the ecology of the species or species groups, to increase our knowledge of the responses of these species to different landscape structures in different geographical regions, and to evaluate the state and distribution of the species in different parts of its distribution ranges.

Based on the results of this study, the following general conclusions can be drawn:

- Heterogeneous landscapes that are mostly composed of natural and semi-natural land cover, as our study region (northeast Estonia), harbour species-rich butterfly, day-active moth, and bumblebee communities.

- The presence of foraging and host plants with high diversity and abundance in the habitat patch and the surrounding landscape may have a significant effect on the composition, abundance, and species richness of pollinating insects in semi-natural meadows.

- The presence of forest in the surrounding landscape of the habitat patch appears to be favourable for butterfly diversity through the creation of shelter, the offering of additional food or host resources, and the offering of warmer microclimatic conditions.

- The higher proportion of meadows and arable land in the

surrounding landscape may negatively affect the species richness and abundance of butterflies. Meadows and fields, which are considered open communities, increase the landscape openness and therefore increase the influence of wind on butterfly behaviour.

- At the local scale, butterflies and day-active moths appear to prefer simplified rather than complex landscapes.

- Habitat patches with an increased interior area appear to be favourable for bumblebee species richness. Interior areas have stable environmental conditions or resources that bumblebees require.

- The proportion of meadow habitat and human settlements, in terms of flower-rich gardens, in the surrounding landscape appears to be favourable for bumblebee species richness because these land covers offer diverse and stable foraging resources and suitable nesting sites.

- The presence of forest and arable land in the surrounding landscape of a habitat patch may negatively affect the species richness and abundance of bumblebees.

- The preferred habitats of the specialist butterfly species Clouded Apollo (*Parnassius mnemosyne*) are dry riparian meadows in forested landscapes. The configuration of the meadow patches along rivers most likely supports the dispersal of the butterfly.

- Despite the decrease in traditional management regimes in Estonia, the observed distribution changes of Clouded Apollo in recent decades allow us to suggest that the availability of semi-natural grasslands, suitable for the butterfly and other pollinating insects remains good.

- Due to its complex habitat requirements, populations of Clouded Apollo are very sensitive to any changes in the quality of the habitats; therefore, the species is a valuable indicator of the state of semi-natural meadows.

- Different insect groups can have different responses to different habitat and landscape factors. Therefore, a protection policy and management practice should not only consider the requirements of one insect group but also should offer a wider range of environmental conditions for several possible organism groups.

- Even if one organism group does not require heterogeneous landscapes, it is important to ensure more diverse environmental conditions through a higher landscape heterogeneity for higher general diversity.

REFERENCES

Aagaard, K. & Hansen, O. 1992. Population studies of *Parnassius mnemosyne* (Lepidoptera) in Sunndalen, Norway. In: Pavlicek, T., Ovaa, A. H. & van der Made, J. G. (ed.), Future of Butterflies in Europe: strategies for survival. Proceedings of the International Congress, held at Wageningen during April 12-15, 1989: 160-166. Agricultural University Wageningen, Wageningen. 326 pp.

Auckland, J.N., Debinski, D.M., Clark, W.R. 2004. Survival, movement, and resource use of the butterfly *Parnassius clodius*. Ecological Entomology 29: 139-149.

Bäckman, J-P. C. & Tiainen, J. 2002. Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera: *Bombus* and *Psithyrus*). Agriculture, Ecosystems and Environment 89: 53-68.

Benton, B.T., Vickery, J.A., Wilson, J.D. 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology and Evolution 18: 182-188.

Bergman, K.-O., Ask, L., Askling, J., Ignell, H., Wahlman, H., Milberg, P. 2008. Importance of boreal grasslands in Sweden for butterfly diversity and effects of local and landscape habitat factors. Biodiversity Conservation 17: 139-153.

Bergström, A. 2005. Oviposition site preferences of the threatened butterfly *Parnassius mnemosyne* - implications for conservation. Journal of Insect Conservation 9: 21-27.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 131: 351-354.

Binzenhöfer, B., Schröder, B., Strauss, B., Biedermann, R., Settele, J. 2005. Habitat models and habitat connectivity analysis for butterflies and burnet moths – the example of *Zygaena carniolica* and *Coenonympha arcania*. Biological Conservation 126: 247–259.

Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Poyry, J., Roberts, S.P.M., Steffan-Dewenter, I., Öckinger, E. 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. Proceedings of the Royal Society B-Biological Sciences 277: 2075–2082.

Bourn, N.A.D. & Thomas, J.A. 2002. The challenge of conserving butterflies at range margins in Europe. Biological Conservation 104: 285–292.

Brückmann, S.V., Krauss, J., Steffan-Dewenter, I. 2010. Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. Journal of Applied Ecology 47: 799-809.

Bryk, F. 1922. "Parnassiana". *Parnassius mnemosyne* L. in Europa. Die estnische Form. Societas Entomologica 37: 5-6.

Carvalheiro, L.G., Kunin, W.E., Keil, P., Aguirre-Gutierrez, J., Ellis, W.N., Fox, R., Groom, Q., Hennekens, S., Van Landuyt, W., Maes, D., Van de Meutter, F., Michez, D., Rasmont, P., Ode, B., Potts, S.G., Reemer, M., Roberts, S.P.M., Schaminee, J., Wallisdevries, M.F., Biesmeijer, J.C. 2013. Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. Ecology Letters 16 (7): 870-878.

Carvell, C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. Biological Conservation 103: 33–49.

Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D., Goulson, D. 2006. Declines in forage availability for bumblebees at a national scale. Biological Conservation 132: 481-489.

Collinge, S.K., Prudic, K.L., Oliver, J.C. 2003. Effects of local habitat characteristics and landscape context on grassland butterfly diversity. Conservation Biology 17 (1): 178-187.

Cranmer, L., McCollin, D., Ollerton, J. 2012. Landscape structure influences pollinator movements and directly affects plant reproductive success. Oikos 121: 562-568.

Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A., Wolters, V. 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. Agriculture Ecosystems & Environment 98: 321–329.

Davis, J.D., Debinski, D.M., Danielson, B.J. 2007. Local and landscape effects on the butterfly community in fragmented Midwest USA prairie habitats. Landscape Ecology 22: 1341–1354.

Debinski, D.M., Ray, C., Saveraid, E.H. 2001. Species diversity and the scale of the landscape mosaic: do scale of movement and patch size affect diversity? Biological Conservation 98: 179–190.

Dennis, R.L.H., Shreeve, T.G., Van Dyck, H. 2006. Habitats and resources: the need for a resource-based definition to conserve butterflies. Biodiversity and Conservation 15: 1943-1966.

Diaz Forero, I. 2011. Influence of abiotic and biotic factors at patch and landscape scale on bumblebees (*Bombus* spp.) in semi-natural meadows. Thesis. Estonian University of Life Sciences, Tartu, 135 pp.

Diekötter, T., Walther-Hellwig, K., Conradi, M., Suter, M., Frankl, R. 2006. Effects of landscape elements on the distribution of the rare bumblebee species *Bombus muscorum* in an agricultural landscape. Biodiversity and Conservation 15: 57-68.

Dover, J. & Settele, J. 2009. The influences of landscape structure on butterfly distribution and movement: a review. Journal of Insect Conservation 13: 3-27.

Dover, J.W., Sparks, T.H., Greatorex-Davies, J.N. 1997. The importance of shelter for butterflies in open landscapes. Journal of Insect Conservation 1: 89–97.

Eiden, G., Kayadjanian, M., Vidal, C. 2000. Capturing landscape structures: Tools. The European Commission. http://ec.europa.eu/agriculture/publi/landscape/ch1.htm. Accessed on 11 March 2013.

Ekroos, J., Heliölä, J., Kuussaari, M. 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. Journal of Applied Ecology 47: 459-467.

Fahrig, L. 2001. How much habitat is enough? Biological Conservation 100: 65–74.

Fauna Europaea 2012. Fauna Europaea version 2.5. URL http://www.faunaeur.org. Accessed on 22 January 2012.

Flynn, D.B.F., Gogol-Procurat, M., Nogeire, T., Molinari, N., Rickers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M., DeClerk, F. 2009. Loss of functional diversity under land-use intensification across multiple taxa. Ecology Letters 12: 22–33.

Forman, R.T.T & Gordon, M. 1986. Landscape ecology. Wiley, New York. 619 p.

Gorbach, V.V. & Kabanen, D.N. 2010. Spatial Organization of the Clouded Apollo Population (*Parnassius mnemosyne*) in Onega Lake Basin. Entomological Review 90: 11–22.

Goulson, D. 2010. Bumblebees: behaviour, ecology and conservation. Second Edition. Oxford University Press, USA. 317 p.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., Knight, M.E. 2005. Causes of rarity in bumblebees. Biological Conservation 122 (1): 1–8.

Goulson, D., Lepais, O., O'Connor, S., Osborne, J.L., Sanderson, R.A., Cussans, J., Goffe, L., Darvill, B. 2010. Effects of land use at a landscape scale on bumblebee nest density and survival. Journal of Applied Ecology 47: 1207-1215.

Goulson, D., Lye, G.C., Darvill, B. 2008. Decline and conservation of bumble bees. Annual Review of Entomology 53: 191-208.

Gratton, P., Konopinski, K., Sbordoni, V. 2008. Pleistocene evolutionary history of the Clouded Apollo (*Parnassius mnemosyne*): genetic signatures of climate cycles and a time-dependent mitochondrial substitution rate. Molecular Ecology 17: 4248-4262.

Haddad, N.M. 1999. Corridor and distance effects on interpatch movements: a landscape experiment within butterflies. Ecological Applications 9: 612-622.

Hagen, M., Wikelski, M., Kissling, W.D. 2011. Space use of bumblebees (*Bombus* spp.) revealed by radio-tracking. PLoS ONE 6 (5): e19997.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford. 313 p.

Hanski, I., Breuker, C.J., Schöps, K., Setchfeld, R., Nieminen, M. 2002. Population history and life history influence the migration rate of female Glanville fritillary butterflies. Oikos 98: 87-97.

Hatfield, R.G. & LeBuhn, G. 2007. Patch and landscape factors shape community assemblage of bumble bees, *Bombus* spp. (Hymenoptera: Apidae) in montane meadows. Biological Conservation 139: 150-158.

Heikkinen, R.K., Luoto, M., Kuussaari, M., Toivonen, T. 2007. Modelling the spatial distribution of a threatened butterfly: Impacts of scale and statistical technique. Landscape and Urban Planning 79: 347-357.

Jauker, F., Diekötter, T., Schwarzbach, F., Wolters, V. 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landscape Ecology 24: 547-555.

Jauker, B., Krauss, J., Jauker, F., Steffan-Dewenter, I. 2013. Linking life history traits to pollinator loss in fragmented calcareous grasslands. Landscape Ecology 28: 107-120.

Jonason, D., Andersson, G.K.S., Öckinger, E., Smith, H.G., Bengtsson, J. 2010. Field scale organic farming does not counteract landscape effects on butterfly trait composition. Agriculture, Ecosystems and Environment 158: 66-71.

Jürivete, U. & Õunap, E. 2008. Estonian Lepidoptera: Catalogue. Estonian Lepidopterologists' Society, Tallinn. 175 p.

Kesküla, T. 1991. Clouded Apollo in Estonia. Estonian Nature 4: 257-258. [In Estonian].

Kesküla, T. & Luig, J. 1997. Phenology and distribution of the Clouded Apollo *Parnassius mnemosyne* (Linnaeus, 1758) in Estonia, with the description of a new subspecies from south-eastern Estonia. Atalanta 28: 17-20.

Kleijn, D. & Van Langevelde, F. 2006. Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. Basic and Applied Ecology 7: 201-214.

Konvička, M. & Kuras, T. 1999. Population structure, behaviour and selection of oviposition sites of an endangered butterfly, *Parnassius mnemosyne*, in Litovelské Pomoraví, Czech Republik. Journal of Insect Conservation 3: 211-223.

Kosior, A., Celary, W., Olejniczac, P., Fijal, J., Król, W., Solarz, W. & Plonka, P. 2007. The decline of bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe. Oryx 41: 79-88.

Krämer, B., Poniatowski, D., Fartmann, T. 2012. Effects of landscape and habitat quality on butterfly communities in pre-alpine calcareous grasslands. Biological Conservation 152: 253-261.

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K.M., Sang, A., Stefanescu, C., Teder, T., Zobel, M., Steffan-Dewenter, I. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecology Letters 13: 597-605.

Krauss, J., Steffan-Dewenter, I., Tscharntke, T. 2003. How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? Journal of Biogeography 30: 889–900.

Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F., Sanjayan, M.A. 1993. Terrestrial arthropod assemblages: their use in conservation planning. Conservation Biology 7 (4): 796-808.

Kreyer, D., Oed, A., Walther-Hellwig, K., Frankl, R. 2004. Are forests potential landscape barriers for foraging bumblebees? Landscape scale experiments with *Bombus terrestris* agg. and *Bombus pascuorum* (Hymenoptera, Apidae). Biological Conservation 116 (1): 111-118.

Kruess, A. & Tscharntke, T. 2002. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. Conservation Biology 16: 1570–1580.

Kukk, T. & Sammul, M. 2006. Area of seminatural Natura 2000 habitat types in Estonia. Year-Book of the Estonian Naturalists' Society 84: 114-158. [In Estonian].

Kumar, S., Simonson, S.E., Stohlgren, T.J. 2009. Effects of spatial heterogeneity on butterfly species richness in Rocky Mountain National Park, CO, USA. Biodiversity and Conservation 18: 739–763.

Kuussaari, M., Heliölä, J., Luoto, M., Pöyry, J. 2007. Determinants of local species richness of day-active Lepidoptera in boreal agricultural landscapes. Agriculture, Ecosystems and Environment 122: 366-376.

Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Avrion, S., Billeter, R., Bugter, R., Hendrickx, F., Burel, F. 2010. Intensification of agriculture, landscape composition and wild bee communities: A large scale study in four European countries. Agriculture, Ecosystems and Environment 137: 143-150.

Lilleleht, V. (chairman). 2008. Estonian Red List of Threatened Species. http://elurikkus.ut.ee/prmt.php?lang=est. Accessed 20 March 2013.

Lindenmayer, D.B. & Fischer, J. 2006. Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis. Island Press, Washington. 329 p.

Luoto, M., Kuussaari, M., Rita, H., Salminen, J., von Bonsdorff, T. 2001. Determinants of distribution and abundance in the clouded apollo butterfly: a landscape ecological approach. Ecography 24: 601-617.

Luoto, M., Kuussaari, M., Toivonen, T. 2002. Modelling butterfly distribution based on remote sensing data. Journal of Biogeography 29: 1027-1037.

Luoto, M., Rekolainen, S., Aakkula, J., Pykälä, J. 2003. Loss of plant species richness and habitat connectivity in grasslands associated with agricultural change in Finland. Ambio 32: 447–452.

MacArthur, R.H. & Wilson, E.O. 1967. The theory of insular biogeography. Princeton University Press. 203 p.

Maes, D., Titeux, N., Hortal, J., Anselin, A., Decleer, K., De Knijf, G., Fichefet, V., Luoto, M. 2010. Predicted insect diversity declines under climate change in an already impoverished region. Journal of Insect Conservation 14: 485-498.

Marini, L., Fontana, P., Battisti, A., Gaston, K.J. 2009. Agricultural management, vegetation traits and landscape drive orthopteran and butterfly diversity in a grassland–forest mosaic: a multi-scale approach. Insect Conservation and Diversity 2: 213-220.

Meglécz, E., Nève, G., Pecsenye, K., Varga, Z. 1999. Genetic variation in space and in time in *Parnassius mnemosyne* (L.) (Lepidoptera) populations in north-east Hungary: implications for conservation. Biological Conservation 89: 251-259.

Meglécz, E., Pecsenye, K., Peregovits, L., Varga, Z. 1997. Allozyme variation in *Parnassius mnemosyne* (L.) (Lepidoptera) populations in North-East Hungary: variation within a subspecies group. Genetica 101: 59-66.

Meier, K., Kuusemets, V., Luig, J., Mander, Ü. 2005. Riparian buffer zones as elements of ecological networks: Case study on *Parnassius mnemosyne* distribution in Estonia. Ecological Engineering 24: 531-537.

Mortelliti, A., Amori, G., Boitani, L. 2010. The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. Oecologia 163: 535–547.

Noordijk, J., Delille, K., Schaffers, A.P., Sykora, K.V. 2009. Optimizing grassland management for flower-visiting insects in roadside verges. Biological Conservation 142: 2097-2130.

Öckinger, E., Lindborg, R., Sjödin, N.E., Bommarco, R. 2012. Landscape matrix modifies richness of plants and insects in grassland fragments. Ecography 35: 259–267.

Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Pöyry, J., Settele, J., Summerville, K.S., Bommarco, R. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecology Letters, 13, 969-979.

Öckinger, E. & Smith, H.G. 2006. Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. Oecologia 149: 526–534.

Öckinger, E. & Smith, H.G. 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. Journal of Applied Ecology 44: 50–59.

Öckinger, E. & Smith, H.G. 2008. Do corridors promote dispersal in grassland butterflies and other insects? Landscape Ecology 23: 27–40.

Ouin, A., Aviron, S., Dover, J., Burel, F. 2004. Complementation/ supplementation of resources for butterflies in agricultural landscapes. Agriculture Ecosystems & Environment 103: 473–479.

Ouin, A. & Burel, F. 2002. Influence of herbaceous elements on butterfly diversity in hedgerow agricultural landscapes. Agriculture Ecosystems & Environment 93: 45–53.

Palang, H., Mander, Ü., Luud, A. 1998. Landscape diversity changes in Estonia. Landscape and Urban Planning 41: 163-169.

Parmesan, C. 1996. Climate and species' range. Nature 382: 765–766.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology. Evolution and Systematics 37: 637-669.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E. 2010. Global pollinator declines: Trends, impacts and drivers. Trends in Ecology and Evolution 25: 345–353.

Potts, S.G., Woodcock, B.A., Roberts, S.P.M., Tscheulin, T., Pilgrim, E.S., Brown, V.K., Tallowin, J.R. 2009. Enhancing pollinator biodiversity in intensive grasslands. Journal of Applied Ecology 46: 369-379.

Pöyry, J., Paukkunen, J., Heliölä, J., Kuussaari, M. 2009. Relative contributions of local and regional factors to species richness and total density of butterflies and moths in semi-natural grasslands. Oecologia 160: 577–587.

Prevedello, J.A. & Vieira, M.V. 2009. Does the type of matrix matter? A quantitative review of the evidence. Biodiversity Conservation 19: 1205–1223.

Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H, Dicks, L.V., Bennet, D., Wright, A., Critchhley, C.N.R., Sherwood, A. 2005. Providing foraging resources for bumblebees in intensively farmed landscapes. Biological Conservation 121: 479-494.

Ries, L. & Debinski, D.M. 2001. Butterflies responses to habitat edges in the highly fragmented prairies of Central Iowa. Journal of Animal Ecology 70: 840-852.

Roland, J., Keyghobadi, N., Fownes, S. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. Ecology 81(6): 1642-1653.

Rosin, Z.M., Myczko, L., Skorka, P., Lenda, M., Moron, D., Sparks, T., Tryjanowski, P. 2012. Butterfly responses to environmental factors in fragmented calcareous grasslands. Journal of Insect Conservation 16: 321-329.

Rundlöf, M., Nilsson, H., Smith, H.G. 2008. Interacting effects of farming practice and landscape context on bumble bees. Biological Conservation 141: 417-426.

Saarinen, K., Valtonen, A., Jantunen, J., Saarnio, S. 2005. Butterflies and day-active moths along road verges: Does road type affect diversity and abundance? Biological Conservation 123: 403–412.

Samways, M.J. 2005. Insect Diversity Conservation. Cambridge University Press, USA. 356 p.

Settele, J., Kudrna, O., Harpke, A., Kuhn, I., van Swaay, C., Verovnik, R., Warren, M., Wiemers, M., Hanspach, J., Hickler, T., Kuhn, E., van Halder, I., Veling, K., Vliegenthart, A., Wynhoff, I. & Schweiger, O. 2008. Climatic Risk Atlas of European Butterflies. BioRisk 1: 1–710.

Shreeve, T.G. & Dennis, R.L.H. 2011. Landscape scale conservation: resources, behaviour, the matrix and opportunities. Journal of Insect Conservation 15: 179–188.

Sjödin, N.E., Bengtsson, J., Ekbom, B. 2008. The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. Journal of Applied Ecology 45: 763-772.

Skórka, P., Settele, J., Woyciechowski, M. 2007. Effects of management cessation on grassland butterflies in southern Poland. Agriculture, Ecosystems and Environment 121: 319-324.

Soga, M. & Koike, S. 2012. Relative importance of quantity, quality and isolation of patches for butterfly diversity in fragmented urban forests. Ecology Research 27: 265-271.

Stefanescu, C., Penuelas, J., Filella, I. 2009. Rapid changes in butterfly communities following the abandonment of grasslands: a case study. Insect Conservation Diversity 2: 261–269.

Steffan-Dewenter, I. & Tscharntke, T. 2000. Butterfly community structure in fragmented habitats. Ecology Letters 3: 449-456.

Stoate, C., Boatman, N.D., Borrahlon, R.J., Carvalho, C.R., de Snoo, G.R., Eden, P. 2002. Ecological impacts of arable intensification in Europe. Journal of Environmental Management 63: 337–365.

Sulcs, A. & Viidalepp, J. 1974. Verbreitung der Großschmetterlinge im Baltikum. I. Tagfalter (Diurna.). Deutsche Entomologische Zeitschrift 21: 353-403. [In German].

Sutcliffe, O.L. & Thomas, C.D. 1996. Open Corridors Appear to Facilitate Dispersal by Ringlet Butterflies (*Aphantopus hyperantus*) between Woodland Clearings. Conservation Biology 10 (5): 1359-1365.

Swihart, R.K. & Moore, J.E. 2004. Conserving Biodiversity in Agricultural Landscapes. Model-Based Planning Tools. Purdue University Press, West Lafayette, Indiana. 336 p.

Taki, H., Kevan, P.G., Ascher, J.S. 2007. Landscape effects of forest loss in a pollination system. Landscape Ecology 22: 1575-1587.

Thomas, J.A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philosophical Transactions of the Royal Society B-Biological Sciences 360: 339–357.

Townsend P.A. & Levey D.J. 2005. An experimental test of whether habitat corridors affect pollen transfer. Ecology 86: 466-475.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A., Thies, C. 2002(a). Characteristics of insect populations on habitat fragments: A mini review. Ecological Research 17: 229–239.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A., Thies, C. 2002(b). Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. Ecological Applications 12 (2): 354-363.

Väisänen, R. & Somerma, P. 1985. The status of *Parnassius mnemosyne* (Lepidoptera, Papilionidae) in Finland. Notulae Entomologicae 65: 109-118.

Välimäki, P. & Itämies, J. 2003. Migration of the clouded Apollo butterfly *Parnassius mnemosyne* in a network of suitable habitats - effects of patch characteristics. Ecography 26: 679-691.

van Swaay, C.A.M., van Strien, A.J., Harpke, A., Fontaine, B., Stefanescu, C., Roy, D., Maes, D., Kühn, E., Õunap, E., Regan, E., Švitra, G., Prokofev, I., Heliölä, J., Settele, J., Pettersson, L., Botham, L., Musche, M., Titeux, N., Cornish, N., Leopold, P., Julliard, R., Verovnik, R., Öberg, S., Popov, S., Collins, S., Goloshchapova, S., Roth, T., Brereton, T., Warren, M. 2013. The European Grassland Butterfly Indicator: 1990-2011. European Environment Agency, Copenhagen, Denmark http://www.eea.europa.eu/publications/the-european-grassland-butterfly-indicator-19902011. Accessed 13 November 2013.

van Swaay, C., Warren, M., Lois, G. 2006. Biotope use and trends of European butterflies. Journal of Insect Conservation 10: 189–209.

Viidalepp, J. 2000. Clouded Apollo (*Parnassius mnemosyne*) in Estonia. Estonian Academy Publishers, Tallinn-Tartu. 40 pp. [In Estonian].

Wallisdevries, M.F., van Swaay, C.A.M. & Plate, C.L. 2012. Changes in nectar supply: A possible cause of widespread butterfly decline. Current Zoology 58 (3): 384-391.

Warren, M.S. & Bourn, N.A.D. 2011. Ten challenges for 2010 and beyond to conserve Lepidoptera in Europe. Journal of Insect Conservation 15: 321-326.

Weibull, A-C. & Östman, Ö. 2003. Species composition in agroecosystems: The effect of landscape, habitat, and farm management. Basic Applied Ecology 4: 349-361.

Westphal, C., Steffan-Dewenter, I., Tscharntke, T. 2006. Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. Oecologia 149: 289-300.

Williams, P.H. & Osborne, J.L. 2009. Bumblebee vulnerability and conservation world-wide. Apidologie 40: 367-387.

Winfree, R., Aguilar, R., Vazquez, D.P., LeBuhn, G., Aizen, M.A. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90 (8): 2068-2076.

Winfree, R., Griswold, T., Kremen, C. 2007. Effect of human disturbance on bee communities in a forested ecosystem. Conservation Biology 21 (1): 213-223.

APPENDIX

List of pollinating insect species observed in 22 semi-natural meadows in north-eastern Estonia (the nomenclature of the species follows Fauna Europaea).

Butterflies and day-active moths

Hesperiidae

Carterocephalus palaemon
Carterocephalus silvicola
Hesperia comma
Heteropterus morpheus
Ochlodes sylvanus
Pyrgus malvae
Thymelicus lineola
Thymelicus sylvestris

Lycaenidae

Aricia (Plebeius) artaxerxes
Aricia (Plebeius) eumedon
Cupido(Everes) argiades
Cupido(Cupido) minimus
Lycaena alciphron
Lycaena dispar
Lycaena hippothoe
Lycaena phlaeas
Lycaena virgaureae
Plebejus (Plebejus) argus
Plebejus (Plebejus) idas
Polyommatus (Polyommatus) amandus
Polyommatus (Polyommatus) icarus
Polyommatus (Cyaniris) semiargus
Pseudophilotes vicrama

Nymphalidae

Aglais urticae
Aphantopus hyperantus
Araschnia levana
Argynnis (Fabriciana) adippe
Argynnis (Mesoacidalia) aglaja
Argynnis (Argyronome) laodice
Argynnis (Argynnis) paphia
Boloria (Clossiana) selene
Brenthis ino
Coenonympha glycerion
Coenonympha hero
Coenonympha pamphilus
Erebia ligea
Euphydryas aurinia
Euphydryas maturna
Hyponephele lycaon
Inachis io
Lasiommata maera
Lasiommata petropolitana
Maniola jurtina
Melitaea athalia
Melitaea diamina
Polygonia c-album
Vanessa atalanta
Vanessa cardui

Papilionidae

Papilio machaon
Parnassius mnemosyne

Pieridae

Aporia crataegi
Gonepteryx rhamni
Leptidea spp
Pieris brassicae
Pieris napi
Pieris rapae

Arctiidae

Atolmis rubricollis
Cybosia mesomella
Diacrisia sannio

Geometridae

Abraxas sylvata
Angerona prunaria
Cabera exanthemata
Cabera pusaria
Camptogramma bilineata
Chiasmia clathrata
Ematurga atomaria
Epirrhoe alternata
Epirrhoe hastulata
Epirrhoe tristata
Idaea serpentata
Lomaspilis marginata
Macaria notata
Odezia atrata
Perizoma albulata
Pterapherapteryx sexalata
Rheumaptera hastata
Scopula floslactata
Scopula immorata
Scopula immutata
Scotopteryx chenopodiata
Siona lineata
Xanthorhoe montanata

Noctuidae

Autographa bractea
Autographa buraetica
Callistege mi
Deltote bankiana
Euclidia glyphica
Hypena proboscidalis
Polypogon tentacularia
Protodeltote pygarga
Tholera decimalis

Sesiidae

Bembecia ichneumoniformis
Synanthedon culiciformis

Sphingidae

Hyles gallii

Zygaenidae

Adscita statices
Zygaena filipendulae
Zygaena lonicerae
Zygaena viciae

Bumblebees and cuckoo bumblebees

Bombus cryptarum
Bombus distinguendus
Bombus hortorum
Bombus hypnorum
Bombus jonellus
Bombus lapidarius
Bombus lucorum
Bombus muscorum
Bombus pascuorum
Bombus pratorum
Bombus ruderarius
Bombus semenoviellus
Bombus schrencki
Bombus soroeensis ssp. soroeensis
Bombus soroeensis ssp. proteus
Bombus soroeensis ssp. soroeensis × *proteus*
Bombus sylvarum
Bombus terrestris
Bombus veteranus
Bombus bohemicus
Bombus campestris
Bombus norvegicus
Bombus rupestris
Bombus sylvestris

SUMMARY IN ESTONIAN

Tolmeldajate elupaiganõudluste mitmekesisus poollooduslikes kooslustes

Tolmeldajad on putukad, kes omavad tähtsat rolli nii põllukultuuride kasvatamisel suurendades nende saagikust kui ka mitmete looduslike taimeliikide paljunemisel. Mitmed tolmeldajatest putukad nagu liblikad ja kimalased on pilkupüüdva välimusega ning suhteliselt kergesti liigini määratavad. Paljud liblika- ja kimalaseliigid on spetsialistid vajades teatud toidutaimi ja elupaiga struktuuri ning seetõttu kasutatakse neid keskkonnatingimuste indikaatoritena.

Viimastel aastakümnetel on märgatud, et liblikate ja kimalaste arvukus on kahanenud, eriti spetisalistliikidel. Tolmeldajate vähenemise põhjusteks on elupaikade hävinemine ja killustumine, põllumajanduslike kemikaalide ülemäärane kasutamine, haigused ning muutused maakasutuses.

Tolmeldajate mitmekesisuse säilitamiseks ja kaitse korraldamiseks on vaja uurida erinevate tolmeldajarühmade või indikaatorliikide levikut ja seda mõjutavaid tegureid, täiendada teadmisi nende ökoloogiast ja seostest elupaiga ning seda ümbritseva maastikuga.

Antud uurimuse üheks eesmärgiks oli hinnata elupaiga ja seda ümbritseva maastiku mõju kimalaste, päevaliblikate ja päeval aktiivsete hämarikuliblikate liigirikkusele ning arvukusele. Selleks valiti 22 poollooduslikku niitu Ida-Virumaal, kus aastatel 2008 ja 2009 määrati uurimisaluste putukate liigiline koosseis, arvukus ja elupaiga ning ümbritseva maastiku peamised parameetrid.

Uurimuse teiseks eesmärgiks oli anda ülevaade Euroopas ohustatud päevaliblika mustlaik-apollo (*Parnassius mnemosyne*) levikust Eestis perioodil 1878-2010. Täiendavalt analüüsiti liblika seoseid elupaiga ja ümbritseva maastikuga.

Käesoleva uurimuse põhjal võib teha järgmised järeldused:

- kimalaste, päevaliblikate ja päeval aktiivsete hämarikuliblikate arvukuse suurendajaks on õitsevate toidutaimede liigirikkus;

- elupaiga tasandil mõjutab kimalaste populatsioone elupaigalaigu siseala osatähtsus, mis stabiilsete ökoloogiliste tingimuste tõttu suurendab kimalaste liigirikkust;

- kimalaste liigrikkust ja arvukust suurendab elupaika ümbritsevas maastikus poollooduslike niitude ja õiterohkete aedade osatähtsus;

- elupaika ümbritsevas maastikus vähendab kimalaste liigirikkust ja arvukust põldude ja metsa osatähtsus;

- päevaliblikate liigirikkusele ja arvukusele avaldab elupaika ümbritsevas maastikus positiivset mõju metsa osatähtsus. Metsaservad pakuvad varju, mitmekesisemaid toitumise ja mikroklimaatilisi tingimusi;

- elupaika ümbritsevas maastikus vähendab päevaliblikate liigirikkust ja arvukust niitude ja põldude osatähtsus. Avatud maastik suurendab tuule mõju liblikate lennuvõimele;

- päevaliblikate ja päeval aktiivsete hämarikuliblikate liigirikkust ja arvukust mõjutab elupaigalaiku ümbritseva maastiku lihtsus. Liblikate mitmekesisus võib olla suurem maastikes, kus erinevate maakattetüüpide arv on väiksem;

- päeval aktiivsete hämarikuliblikate liigirikkusele ja arvukusele avaldab elupaika ümbritsevas maastikus positiivset mõju põldude, niitude ja metsa osatätsus;

- perioodil 1878-2010 on mustlaik-apollo oma leviala Eestis laiendanud, eriti just Kirde- ja Kagu-Eestis. Hoolimata poollooduslike niitude pindala vähemisest viimastel aastakümnetel, võib oletada, et Eestis on hetkel veel piisavalt sobilikke elupaiku nii mustlaik-apollole kui ka teistele tolmeldajatele;

- mustlaik-apollo eelistab elupaigana kuivasid jõgede äärseid niitusid, mis paiknevad metsamaastikus. Liblika röövik toitub valdavalt lehtmetsa ja lepikute all kasvavast harilikust lõokannusest. Valmik seevastu väldib metsa, kuid vajab õiterikkal avatud niidul puurinde lähedust, mis vähendab tuule mõju liblika lennuaktiivsusele;

- kuna mustlaik-apollo on elupaiga spetsialist, siis võib liblikat käsitleda elupaiga kvaliteeti iseloomustava indikaatorliigina. Silmapaistva välimuse tõttu sobiks mustlaik-apollo lipuliigiks poollooduslikes kooslustes tolmeldajate mitmekesisuse kaitsmisel.

Antud uurimus näitas, et kimalased ja liblikad reageerivad erinevalt elupaika ja seda ümbritsevat maastikku iseloomustavatele näitajatele. Tolmeldajate efektiivse kaitse korraldamisel ei tohiks arvestada ainult ühe putukarühma nõudlustega, vaid tuleks säilitada või luua mitmekesised keskkonnatingimused, mis tagab erinevate tolmeldajarühmade liigirikkuse.

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I

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Pollinator richness and abundance in Northeast Estonia: bumblebees, butterflies and day-flying moths

Isabel Diaz-Forero*, Ave Liivamägi, Valdo Kuusemets and Jaan Luig

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Abstract. We studied diversity and abundance of three groups of pollinators: bumblebees, butterflies and day-flying moths, in Ida-Viru County, Estonia. The field work was done during the summers of 2008 and 2009, in 22 semi-natural meadows located across Northeast Estonia. In total, we found 22 species of bumblebees (gen. *Bombus*), including 5 species of cuckoo bumblebees, 56 species of butterflies and 42 species of day-flying moths. We recorded 597 individuals of bumblebees, 768 individuals of butterflies and 330 individuals of day-flying moths in our study sites. We analysed differences between years (2008 and 2009) for the species richness and abundance of bumblebees, butterflies and day-flying moths; the relationships between insect species richness and area of meadow, the total number of species per meadow and the local abundance of each species separately. We found significant differences between bumblebee richness and abundance in 2008 and 2009, and between butterfly abundance at the same years. These differences may be due to more favourable conditions: warmer and dryer weather in the second year. We found no significant relationships between area of meadow and species richness of bumblebees, butterflies and day-flying moths; however, when we analysed the abundance of each species separately, we found that two species of bumblebees, i.e. *B. pascuorum* and *B. schrencki*, and one species of day-flying moths, i.e. *Chiasmia clathrata*, were negatively related with area of meadow. Although, Northeast Estonia is a region that has been environmentally affected by mining activities and the presence of power plants, it could be considered an important area that supports a significant richness and abundance of pollinators across its territory.

Key words: insects, species richness, semi-natural meadows, *Bombus*, Lepidoptera, Ida-Virumaa.

Authors' address: Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi, 5, 51014 Tartu, Estonia, *e-mail: isabel.diaz@emu.ee

Introduction

Grasslands are the most species-rich habitats in European landscapes. Insects constitute an important part of the biodiversity of semi-natural grasslands (Öckinger & Smith, 2007), as they provide unique ecosystem services in the form of nutrient cycling and pollination. Insects are also important environmental indicators because they respond to climatic and management changes faster than plants, which they

need for food and reproduction. Pollinator diversity in semi-natural grasslands is at risk mainly because of the intensification of farming practices (i.e. increased use of fertilisers and pesticides) (Carvell, 2002; Mänd *et al*., 2002; Goulson *et al*., 2006; Holzschuh *et al*., 2008 Xie *et al*., 2008), abandonment of traditional agricultural land use practices (e.g. mowing, grazing, etc.) and successive transformation of remnants into forest. The remaining semi-natural grasslands become more fragmented in the landscape context. All those factors are significantly affecting the diversity of insect communities inhabiting semi-natural grasslands (Cozzi *et al*., 2008; Bergman *et al*., 2008; Sjödin *et al*., 2008).

The loss of pollinators has been an important topic during recent years. There are a lot of articles describing that many bumblebee and butterfly species have undergone significant range declines in different European countries (Mänd *et al*., 2002; Kells & Goulson, 2003; Goulson *et al*., 2006; Williams & Osborne, 2009). In contrary to the most of Europe, there are relatively few studies that have reported increases of butterflies in their abundance and distribution (Kuussaari *et al*., 2007). They observed that increasing trends and expansions of butterflies are generally associated with climate change (Oliver et al., 2009). There is little information on density changes of different species of bumblebees. Some bumblebee species have decreased drastically, but some other species have increased (Goulson *et al*., 2006).

We studied diversity and abundance of three groups of pollinators: bumblebees, butterflies and day-flying moths. The main objective of our research was to determine the species richness and abundance of these three groups of insects in 22 meadows located in Northeast Estonia. We examined the differences between years (2008 and 2009) for the species richness and abundance of bumblebees, butterflies and day-flying moths; and the relationship between insect species richness and area of meadow, analysing first, the total number of species per meadow, and then, the abundance of each species separately.

Materials and methods

Study region

Ida-Viru is a county located in the Northeastern part of Estonia. The total area of our study region is 3364 km2, which represents 7.4% of the total area of Estonia. The areas of the selected meadows ranged from 0.10 to 3.83 ha.

Ida-Virumaa is a region affected mostly by mining activities as it contains large deposits of oil shale, a mineral used for power generation in Estonia. The landscape in the region is mainly dominated by forests, grasslands and arable land, and in a lower proportion, by mires and fresh water bodies. Study sites were chosen in Northeast Estonia with grasslands situated in coastal areas, in forested landscapes and in flooded meadows.

Field work

We visited 22 semi-natural meadows in 2008 and 2009, located in Ida-Viru county. In both years, we sampled each meadow two times. Field works took place in June, July and August, which are the warmest months of the year. Insect counts were done during approximately 45 minutes systematic walking surveys (Kumar *et al*., 2009); during the warmer time of the day, between 11:00 h and 16:00 h; and when the weather conditions were suitable, i.e. temperature was above 18 ºC and wind speed was less than 5 by Beaufort scale. The number of species and individuals of the three insect

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groups were determined by sight at each meadow. When the observer could not identify the species, the individual was caught with an insect net for later identification. The nomenclature of the insects follows Fauna Europaea Web Service (2004).

Weather conditions

In our study area, the closest weather station is Jõhvi that is situated in the middle of the region. The average air temperature per month was higher in 2009, compared with the previous year. We found larger differences between the sums of precipitation: in June, it was higher in 2008 than in 2009 (128 mm and 112 mm, respectively); the same trend was observed in August, with a heavy rain period in 2008 that reached 242 mm (96 mm in 2009); in May the sum of precipitation was similar in both years (28 mm in 2008 and 33 mm in 2009); and in July the sum of precipitation was higher in 2009 than in 2008 (139 mm and 55 mm, respectively). In general, the second year of field work, 2009, had more sunny days and favourable weather conditions for insects.

Statistical analyses

In our study, Pearson's correlation tests were performed to analyse the relationship between area of meadow and insect species richness, using first, the total number of species per meadow, and then, the local abundance of each species separately. In addition, we examine the non-parametric relations between the same variables using the Spearman Rank Order correlations.

We conducted dependent samples (paired) t-tests in order to evaluate the differences between number of individuals and species in 2008 and 2009 for the three groups of insects separately: bumblebees, butterflies and day-flying moths. We used the software STATISTICA 9 for all the statistical analyses.

Results

Bumblebee richness and abundance

We recorded a total of 22 species of bumblebees (gen. *Bombus*), including 5 species of cuckoo bumblebees (subgen. *Psithyrus*). In Estonia, there are 22 species of bumblebees and 7 species of cuckoo bumblebees. An average of 10.7 species and 27.1 individuals of bumblebees per study site were found (Figs. 1a–1b). We counted a total of 597 individuals in our study sites: 207 in 2008 and 390 in 2009. From the total number of individuals of bumblebees found, 363 were workers, 150 males and 84 females. The bumblebee species with the highest number of individuals were *B. pascuorum*, *B. lucorum* and *B. ruderarius* with 140, 70 and 58 individuals, respectively (Fig. 2a). Together with *B. cryptarum,* these species were also the most common bumblebees in the area, as they were found in most of the study sites. On the other hand, the two rarest bumblebee species with the lowest abundance were *B. muscorum* and *B. distinguendus*.

We found five species of long-tongued bumblebees: *B. distinguendus*, *B. hortorum, B. ruderarius, B. sylvarum,* and *B. pascuorum*; and eight species of short-tongued bumblebees: *B. cryptarum*, *B. lapidarius*, *B. lucorum*, *B. terrestris*, *B. hypnorum*, *B. jonellus*, *B. pratorum* and *B. soroeensis* (http://www.nhm.ac.uk). The other species of bumblebees found have a mid-length tongue. Three species: *B. distinguendus, B. muscorum* and *B. soroeensis* are included in the Estonian Red List of Threatened Species (http://elurikkus.ut.ee).

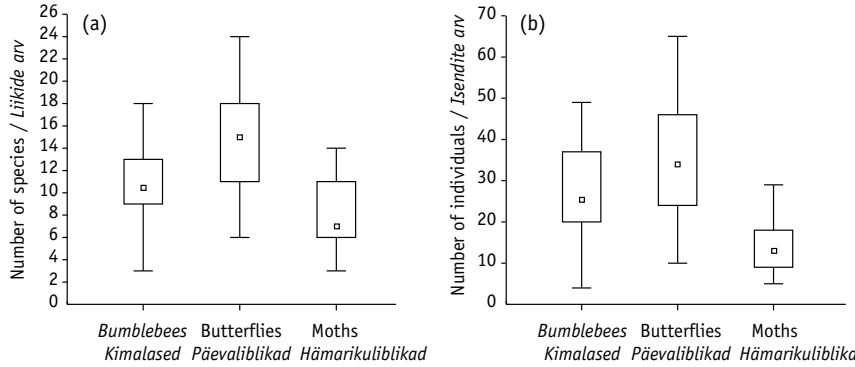


Figure 1. Box-plots showing total number of (a) species and (b) individuals of bumblebees, butterflies and moths found in the study area.

Joonis 1. Karpdiagrammil (a) liikide ja (b) isendite koguarvu jaotumine erinevates putukarühmades.

The places with the highest richness of bumblebees were Kalvi with 18 species, and Soldina, Narva Karjäär and Pannjärve with 15 species each; and the places with the lowest number of species were Valaste and Raadna Oja, with 2 and 3 species of bumblebees, respectively (Table 1).

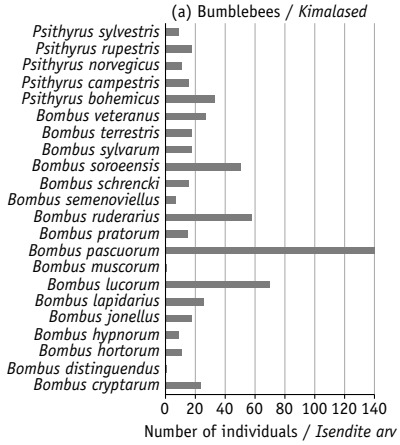
We found significant differences between species richness and abundance of bumblebees in 2008 and 2009 ($t = 6.0$, $df = 21$, $p = 0.000006$; $t = 5.7$, $df = 21$, $p = 0.00001$, respectively): the number of species and individuals was significantly higher in the second year.

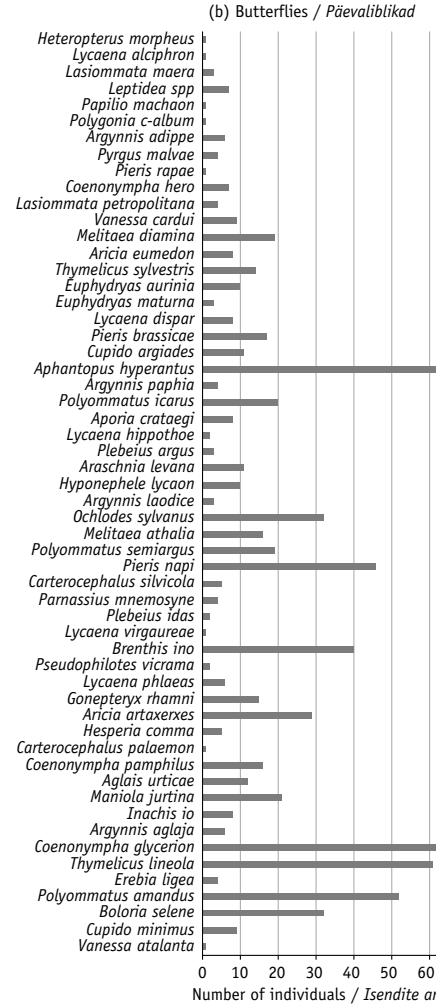
Concerning the relations between bumblebee species richness and area of meadow, we found no significant correlations between the variables ($p > 0.05$). However, when the local abundance of each species and area of meadow were analysed, using non-parametric (Spearman rank order) correlations, we found that two species of bumblebees, i.e. *B. pascuorum* and *B. schrencki*, were both negatively correlated with area of meadow ($r = -0.5$, $n = 22$, $p < 0.05$).

Butterfly richness and abundance

A total of 768 individuals of butterflies belonging to 56 species were found in our study sites: 333 individuals in 2008 and 435 individuals in 2009. We found an average of 15.6 species and 34 individuals of butterflies per study site (Figs. 1a–1b). The most abundant species found were *Coenonympha glycerion* with 65 individuals, *Aphantopus hyperantus* with 62 individuals and *Thymelicus lineola* with 61 individuals (Fig. 2b). The most common species found in our study sites were *Thymelicus lineola*, *Aphantopus hyperantus* and *Pieris napi*. The species with the lowest abundance were *Vanessa atalanta*, *Carterocephalus palaemon*, *Lycaena virgaureae*, *Pieris rapae*, *Polygonia c-album*, *Papilio machaon*, *Lycaena alciphron* and *Heteropterus morpheus*.

In our study region, we found 5 species of butterflies that are protected under the EU Habitat Directive Natura 2000 (http://elurikkus.ut.ee): *Parnassius mnemosyne*, *Lycaena dispar*, *Euphydryas maturna*, *Euphydryas aurinia* and *Coenonympha hero*.





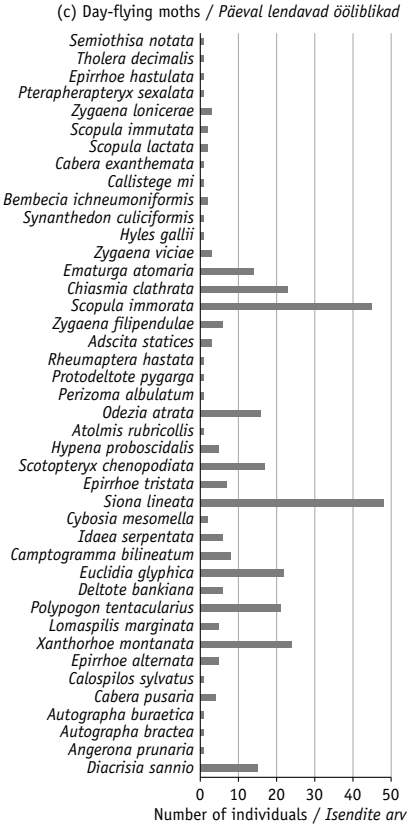


Figure 2. Total number of individuals per species of (a) bumblebees, (b) butterflies and (c) day-flying moths.

Joonis 2. Uurimisalalt püütud isendite arvu jaotumine liigiti kimalastel (a), päevaliblikatel (b) ja päeval aktiivsetel hämarikuliblikatel (c).

Table 1. Number of species and individuals of bumblebees, butterflies and day-flying moths. Notations: SR – total species richness, IND – total number of individuals.

Tabel 1. Kimalaste, päevaliblikate ja päeval aktiivsete hämarikuliblikate isendite (IND) ja liikide (SR) arv uurimisaladel.

#	Study site *Uurimisalad*	Area (ha) *Pindala (ha)*	Geographic coordinates *Geograafilised koordinaadid*	Bumblebees *Kimalased* SR	Bumblebees *Kimalased* IND	Butterflies *Päevaliblikad* SR	Butterflies *Päevaliblikad* IND	Day-flying moths *Päeval aktiivsed hämarikuliblikad* SR	Day-flying moths *Päeval aktiivsed hämarikuliblikad* IND
1	Smolnitsa	0.12	59°00′38″N 27°36′52″E	14	37	24	46	6	9
2	Kuningaküla	0.69	59°07′35″N 27°48′10″E	12	49	14	31	6	7
3	Raadna Oja	3.38	58°58′53″N 27°07′31″E	3	7	15	30	8	11
4	Lemmaku	3.61	59°00′20″N 27°09′36″E	9	22	16	25	6	10
5	Mäetaguse	3.65	59°13′40″N 27°19′44″E	12	21	17	27	12	29
6	Atsalama	1.47	59°14′31″N 27°23′12″E	9	31	22	52	14	32
7	Kurtna	1.12	59°14′59″N 27°33′58″E	8	15	16	45	13	32
8	Pannjärve	0.48	59°17′18″N 27°33′24″E	15	36	29	53	12	21
9	Tagajõgi_R	0.23	59°04′54″N 27°04′37″E	11	22	11	24	11	16
10	Tagajõgi_O	1.02	59°07′12″N 26°59′26″E	9	22	18	51	5	14
11	Piilse	3.87	59°14′09″N 26°59′31″E	7	15	8	16	11	23
12	Kalvi	3.32	59°28′52″N 26°46′36″E	18	40	10	17	7	9
13	Kalvi_Oru	1.23	59°27′34″N 26°48′24″E	10	18	6	10	11	14
14	Liimala	1.42	59°26′06″N 26°59′01″E	12	37	11	27	4	5
15	Moldova	1.91	59°25′59″N 27°04′11″E	13	28	24	65	6	8
16	Valaste	0.89	59°26′18″N 27°25′20″E	2	4	8	11	3	6
17	Päite	1.06	59°24′16″N 27°42′02″E	10	20	11	21	7	13
18	Udria	0.82	59°23′36″N 27°54′07″E	10	33	15	39	9	17
19	Soldina	0.26	59°23′01″N 28°04′43″E	15	45	14	37	7	18
20	Auvere	3.59	59°20′36″N 27°58′20″E	9	23	15	40	7	13
21	Narva_K	0.91	59°15′52″N 27°49′15″E	15	41	20	45	8	12
22	Meriküla	1.37	59°24′46″N 27°57′12″E	13	31	18	56	7	11

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Pannjärve, Moldova and Narva Karjäär were sites with the highest number of species of butterflies with 29, 24 and 20 species, respectively. On the contrary, the sites with the lowest butterfly diversity were Kalvi Oru with 6 species, and Valaste and Piilse with 8 species each (Table 1).

According to the t-tests results, we found significant differences between number of individuals of butterflies in 2008 and 2009 ($t = 3.0$, $df = 21$, $p = 0.007$): it was higher in the second year. However, there was no significant difference between years in the case of butterfly species richness ($p > 0.05$).

From the analysis of the relationship between butterfly species richness and area of meadow, we found no significant correlations ($p > 0.05$). The same results were obtained when we analysed the relations between local abundance of each species and area of meadow.

Day-flying moth richness and abundance

We found a total of 42 species and 330 individuals of day-flying moths in our study sites. 179 individuals were recorded in 2008 and 151 in 2009. In average, we found 8.2 species and 13 individuals of moths per study site (Figs. 1a–1b). The most abundant species found in Ida-Virumaa were *Siona lineata* and *Scopula immorata*, with 48 and 45 individuals, respectively (Fig. 2c). These two were also the most common species found in the majority of our study sites, along with *Euclidia glyphica*.

Among the species of day-flying moths, we found that *Rheumaptera hastata* is considered a species of least concerned in the Estonian Red List of Threatened Species (http://elurikkus.ut.ee).

The places with the highest diversity of day-flying moths were: Atsalama hoiuala with 14 species, Kurtna Särgjärv with 13, and Pannjärve and Mäetaguse, both with 12 species (Table 1).

Our results from t-tests show that there were no significant differences between moth diversity and abundance in 2008 and 2009 ($p > 0.05$).

We also found that species richness of moths was not significantly correlated with area of meadow ($p > 0.05$). In the case of local abundance of each species of moths, we found that there was a negative non-parametric (Spearman rank order) correlation between the species *Chiasmia clathrata* and area of meadow ($r = -0.4$, $n = 22$, $p < 0.05$).

Discussion

Semi-natural habitats constitute areas of great value for pollinators, particularly bumblebees and butterflies, mainly due to the availability of a broad range of flowering resources and nesting places (Svensson *et al*., 2000; Kells & Goulson, 2003; Öckinger & Smith, 2007). Estonia has a very mosaic landscape with a mixture of forest, agricultural land and semi-natural areas (Mänd *et al.*, 2002). Although Ida-Viru is a region mainly dominated by forest (which constitutes 58% of the whole area), semi-natural meadows represent important targeting areas for biodiversity conservation.

Among the bumblebee species found in Northeast Estonia, *B. pascuorum* was the most common and abundant species. This is a very common bumblebee species, particularly in Europe and northern Asia (http://www.nhm.ac.uk). In a study done in Estonia by Mänd *et al*. (2002), they also found that *B. pascuorum* and *B. lucorum* were some of the most dominant bumblebee species in semi-natural habitats, and *B. muscorum* was one of the rarest species. The extremely rare and declining bumblebees

B. muscorum and *B. distinguendus* (mid-tongued and long-tongued species, respectively), are late-emerging species that are associated with unimproved grasslands (Goulson *et al.*, 2005). In our study, these species were found in places located close to fresh waterbodies. This is consistent with the results obtained by Goulson *et al.* (2006), in which several declining bumblebee species were found mostly in coastal areas. They suggested that a possible explanation for the distribution of these rare species was that coastal areas are less impacted by agriculture and intensive farming (Goulson *et al.*, 2006).

Bumblebee species richness and abundance was higher in 2009, compared with 2008; it may be due to more favourable weather conditions in the second year. The same could apply in the case of butterfly abundance, as the weather in the summer of 2008 was colder and more windy than in 2009.

The butterfly species *Coenonympha glycerion* was the most abundant species found in our study area. However, in countries like Finland, it has shown a consistent decline in semi-natural grasslands (Kuussaari *et al.*, 2007; Pöyry *et al.*, 2009). Pöyry *et al.* (2009) explained that this species has shown a declining trend in Finland mainly due to decreasing availability of habitats. This species has been also commonly found in bog habitats (Kulfan *et al.*, 1997). Other butterfly species that we found to be dominant in our study sites (i.e. *Aphantopus hyperantus*, *Thymelicus lineola* and *Pieris napi*) are also considered common species in Finish agricultural landscapes (Pöyry *et al.*, 2005; Kuussaari *et al.*, 2007). Contrary to our results, in Finland *Pieris napi* has been commonly found in arable field margins (Kuussaari *et al.*, 2007).

The most abundant species of day-flying moths in our study sites were *Siona lineata* and *Scopula immorata*. According to Pöyry *et al.* (2005), *Siona lineata* is commonly found in old and abandoned pastures, while *Scopula immorata* seems to prefer the second type of habitat.

Among our study sites, we found that Pannjärve was the place with one of the highest species richness of bumblebees, butterflies and day-flying moths. The study site Narva Karjäär was also found to have one of the highest numbers of species of bumblebees and butterflies. On the other hand, Valaste was one of the places with the lowest number of species of bumblebees and butterflies. This place is located in the northern part of Ida-Viru county, very close to the Gulf of Finland in the Baltic sea.

Although area of meadow did not seems to be an important factor for the total species richness of our three groups of pollinators, there seems to be a negative influence on some species of bumblebees (i.e. *B. pascuorum* and *B. schrencki*) and day-flying moths (i.e. *Chiasmia clathrata*).

Conclusion

Even though, Northeast Estonia is a region that has been environmentally affected by mining activities and the presence of power plants, it could be considered an important area for conservation of some species of pollinators, as it supports a significant richness and abundance of bumblebees, butterflies and day-flying moths across its territory. The mosaic landscape with forests, grasslands and arable areas, and the presence of semi-natural meadows in the region seems to be favourable for pollinators.

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References

Bergman, K-O., Ask, L., Askling, J., Ignell, H., Wahlman, H., Milberg, P. 2008. Importance of boreal grasslands in Sweden for butterfly diversity and effects of local and landscape habitat factors. – Biodiversity and Conservation, 17, 139–153.

Carvell, C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. – Biological Conservation, 103, 33–49.

Commission for Nature Conservation of the Estonian Academy of Sciences. 2001-2002. Estonian Red List of Threatened Species. [WWW document]. – URL http://elurikkus.ut.ee.

Cozzi, G., Müller, C. B., Krauss, J. 2008. How do local habitat management and landscape structure at different spatial scales affect fritillary butterfly distribution on fragmented wetlands? – Landscape Ecology, 23, 269–283.

European Commission. Habitats Directive (92/43/EEC) European Commission (1992/1995). Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. [WWW document]. – URL http://europa.eu.

Fauna Europaea Web Service. 2004. Fauna Europaea version 1.1. [WWW document]. – URL http://www.faunaeur.org.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. 2006. Biotope associations and the decline of bumblebees (*Bombus* spp.). – Journal of Insect Conservation, 10, 95–103.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., Knight, M.E. 2005. Causes of rarity in bumblebees. – Biological Conservation, 122, 1–8.

Holzschuh, A., Steffan-Dewenter, I., Tscharntke, T. 2008. Agricultural landscapes with organic crops support higher pollinator diversity. – Oikos, 117, 354–361.

Kells, A.R., Goulson, D. 2003. Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. – Biological Conservation, 109, 165–174.

Kulfan, M., Degma, P., Kalivoda, H. 1997. Lepidoptera of different grassland types across the Morava floodplain. – Journal of Research on the Lepidoptera, 34, 39–47.

Kumar, S., Simonson, S.E., Stohlgren, T.J. 2009. Effects of spatial heterogeneity on butterfly species richness in Rocky Mountain National Park, CO, USA. – Biodiversity and Conservation, 18, 739–763.

Kuussaari, M., Heliölä, J., Pöyry, J., Saarinen, K. 2007. Contrasting trends of butterfly species preferring semi-natural grasslands, field margins and forest edges in northern Europe. – Journal of Insect Conservation 11, 351–366.

Mänd, M., Mänd, R., Williams, I.H. 2002. Bumblebees in the agricultural landscape of Estonia. – Agriculture, Ecosystems & Environment, 89, 69–76.

Natural History Museum. 2011. Research and curation. [WWW document]. – URL http://www.nhm.ac.uk.

Oliver, T., Hill, J.K., Thomas, C.D., Brereton, T., Roy, D.B. 2009. Changes in habitat specificity of species at their climatic range boundaries. – Ecology Letters, 12, 1091–1102.

Öckinger, E., Smith, H.G. 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. – Journal of Applied Ecology, 44, 50–59.

Pöyry, J., Lindgren, S., Salminen, J., Kuussaari, M. 2005. Responses of butterfly and moth species to restored cattle grazing in semi-natural grasslands. – Biological Conservation, 122, 465–478.

Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M., Saarinen, K. 2009. Species traits explain recent range shifts of Finnish butterflies. – Global Change Biology, 15, 732–743.

Sjödin, N. E., Bengtsson, J., Ekbom, B. 2008. The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. – Journal of Applied Ecology, 45, 763–772.

Svensson, B., Langerlöf, J., Svensson, B.G. 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. – Agriculture, Ecosystems & Environment, 77, 247–255.

Williams, P.H., Osborne, J.L. 2009. Bumblebee vulnerability and conservation world-wide. – Apidologie, 40, 367–387.

Xie, Z., Williams, P.H., Tang, Y. 2008. The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan. – Journal of Insect Conservation, 12, 695–703.

Kolme tolmeldajaterühma: kimalased, päevaliblikad ja päeval aktiivsed hämarikuliblikad, liigirikkus ja arvukus Ida-Virumaal

Isabel Diaz-Forero*, Ave Liivamägi, Valdo Kuusemets ja Jaan Luig

Kokkuvõte

Töö eesmärgiks oli uurida kolme tolmeldajate rühma: kimalased, päevaliblikad ja päeval aktiivsed hämarikuliblikad, liigirikkust ja arvukust Ida-Virumaal. Välitööd tehti aastatel 2008 ja 2009 22-l poollooduslikul niidul. Kimalasi leiti 22 liiki (gen. *Bombus*), sealhulgas 5 liiki kägukimalasi (subgen. *Psithyrus*), 597 isendit. Kõige arvukamad liigid olid *B. pascuorum*, *B. lucorum* and *B. ruderarius*. Päevaliblikaid leiti 56 liiki ja 768 isendit, kõige arvukamad liigid olid *Coenonympha glycerion*, *Aphantopus hyperantus* ja *Thymelicus lineola*. Päeval aktiivseid hämarikuliblikaid leidsime 42 liiki ja 330 isendit, kõige arvukamad liigid olid *Siona lineata* ja *Scopula immorata*.

Kimalaste liigirikkus ja arvukus ning liblikate arvukus erinesid statistiliselt oluliselt aastatel 2008 ja 2009. See võis olla põhjustatud erinevate aastate ilmastikutingimuste erinevustest, kuivõrd 2009. aasta oli kuivem ja soojem.

Elupaiga suurus ei avaldanud statistiliselt usaldusväärset mõju uuritud tolmeldajate rühmade liigirikkusele. Samas omas elupaiga suurenemine negatiivset mõju mõningate liikide, nagu *B. pascuorum, B. schrencki* ja *Chiasmia clathrata* arvukusele.

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Influence of habitat and landscape on butterfly diversity of semi-natural meadows within forest-dominated landscapes

Ave Liivamägi[1], Valdo Kuusemets, Tanel Kaart[2], Jaan Luig and Isabel Diaz-Forero

Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5, 51014 Tartu, Estonia; [1] e-mail: ave.liivamagi@emu.ee

[2] Institute of Veterinary Medicine and Animal Sciences, Estonian University of Life Sciences, Kreutzwaldi 62, 51014 Tartu, Estonia

Abstract

1. This study investigates how butterfly communities are influenced by habitat and landscape factors in forest-dominated landscapes. The abundance and species richness of butterflies were determined in 22 semi-natural meadows located in north-eastern Estonia.
2. A correlation analysis, partial least squares (PLS) analysis and stepwise forward-selection multiple regression analysis were applied for habitat parameters and the surrounding landscape at four spatial scales, i.e. 250, 500, 1000 and 2000 m radius.
3. We found a positive correlation between the proportion of forest and total butterfly species richness at a 250 m radius scale. Contrary to expectation, the amount of meadow area in the surrounding landscape negatively influenced butterfly species richness and abundance.
4. Our results emphasise the importance of both the surrounding landscape and habitat characteristics for butterfly species richness. Because butterfly communities are composed of individual species with different habitat requirements, diverse habitats and landscape configurations should be applied in insect conservation and management.

Key words. Lepidoptera, species richness, patch quality, land cover types, landscape indices, heterogeneity, farmland abandonment.

Introduction

The population trends of many European butterflies have been shown to be decreasing (van Swaay *et al*., 2006). A recent report states that the population of grassland butterfly species declined by almost 50% from 1990 to 2011 (van Swaay *et al*., 2013). Furthermore, butterfly specialist species have declined more rapidly than generalist species (van Swaay *et al*., 2006). The causes of population decline are different for a particular species and region, but the main drivers are deterioration of habitat quality (Mortelliti *et al*., 2010), increased fragmentation and loss of habitat patches (Krauss *et al*., 2010), increased agricultural intensification (Stoate *et al*., 2002; Benton *et al*., 2003; Luoto *et al*., 2003), climate change (Parmesan, 2006; Maes *et al*., 2010) and, presumably, complex interactions of all these factors (Shreeve & Dennis, 2011).

To counteract the severe decline in insect biodiversity in agricultural landscapes, many studies have investigated the relationship between species diversity patterns and the preferred habitat conditions in different landscape structures, and this at different spatial scales (Bergman *et al*., 2008; Cozzi *et al*., 2008; Kumar *et al*., 2009; Marini *et al*., 2009; Öckinger *et al*., 2012). In general, several studies confirm correlations between butterfly species richness and certain landscape and habitat metrics (Weibull & Östman, 2003; Öckinger & Smith, 2006; Rossi &

van Halder, 2010). Some early studies concentrated mostly on the relationships between habitat patch characteristics (area, shape, quality, etc.) and species richness (Thomas *et al*., 2001), whereas more recent studies tend to investigate insect diversity in relation to both local habitat characteristics and landscape configuration (Dauber *et al*., 2003; Krauss *et al*., 2003; Öckinger & Smith, 2006; Davis *et al*., 2007; Krämer *et al*., 2012). Moreover, some recent studies emphasise the importance of life-history traits in predicting species richness (Pöyry *et al*., 2009; Öckinger *et al*., 2010), mainly because individual species perceive and use the landscape in different ways.

However, within this research area, a consensus is still lacking. The effects of the surrounding landscape seem to be complex and can depend on local conditions. It has been suggested that the relationship between species diversity and the adjacent landscape partly depends on landscape heterogeneity and quality (Fahrig, 2001; Tscharntke *et al*., 2005; Bergman *et al*., 2008) and evolutionary history (Bergman *et al*., 2004). However, despite the large variability in results, there are some general patterns in butterfly species' responses to their habitats being altered in transformed landscapes. It has been suggested that, in highly fragmented and homogeneous landscapes, butterfly communities will be dominated by mobile generalists (Kuussaari *et al*., 2007b; Ekroos *et al*., 2010; Öckinger *et al*., 2010).

Understanding the relationship between butterflies and the surrounding landscape is relevant to the conservation of this group of flower-visiting insects. Thus far, most studies have been conducted in open agricultural areas. However, more needs to be known about the relationship between butterflies and the surrounding environment in areas with more natural habitats, particularly those with forest landscapes that can fragment habitats.

In this study, we investigate how butterfly diversity and abundance in forest dominated areas of north-eastern Estonia is influenced by patch-scale factors and the presence of different habitat types in the surrounding landscape at multiple spatial scales.

Materials and methods

Study region

The study was conducted in Ida-Virumaa County, located in northeast Estonia (Fig. 1). The region covers an area of 336,400 ha, accounting for approximately 7.5% of the total area of Estonia. The study region's landscape is dominated primarily by forests (coniferous and mixed forests comprised mostly of birches, pines and spruces), which occupy approximately 58.0% of the territory in the region. In lesser proportions, the region is covered by arable land (12.4%), young forest (6.5%), meadows (5.7%) and other land cover types (human settlements, mires, bodies of fresh water, etc.).

Butterfly survey

The field study was conducted during 2008 and 2009 in 22 semi-natural meadows that differed in size (0.10-3.83 ha, mean=1.66 ha), shape, vegetation characteristics and surrounding landscapes. Recordings of butterflies (Papilionoidea and Hesperioidea) were conducted twice a year on each site between June and the first half of August. Insect counts were conducted for approximately 45-60 minutes during each visit using systematic walking surveys (Kumar *et al*., 2009). The field work was performed during the warmer hours of the

day, between 10:00 and 16:00, under suitable weather conditions. Species type and individual butterflies were visually identified in each meadow. However, when the observer could not identify the species, the insects were caught by hand net to later identify in the laboratory. Species of the genus *Leptidea* (*L. sinapis* and *L. reali*) were grouped together. The nomenclature of the butterfly species follows Fauna Europaea (2012).

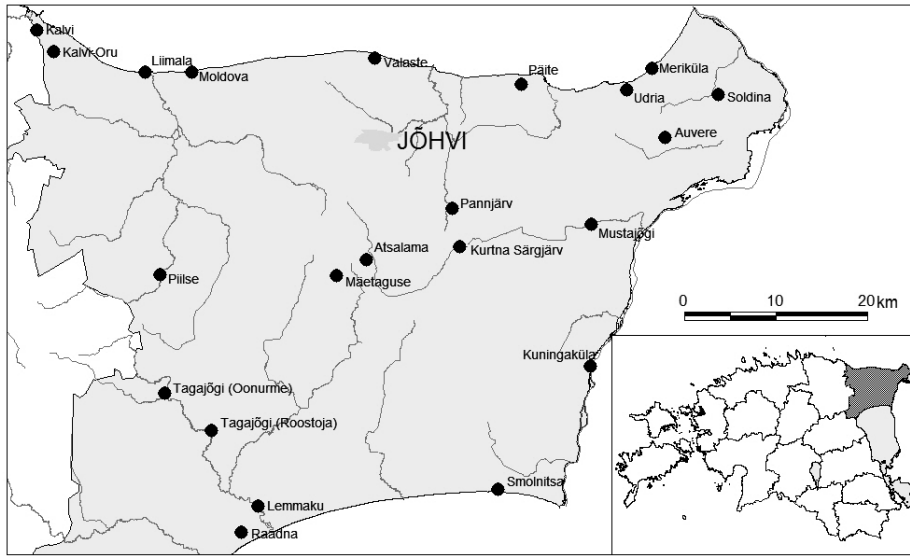

Fig. 1. The study region is located in the north-eastern part of Estonia. The locations of study sites are shown by black dots.

Variables at the patch and landscape scale

At the patch scale, we determined the number of species of plants that were flowering at the time of the surveys (SRFFlowPlants), estimated the percent cover of plants that were flowering (AvCoverFP) and measured vegetation height (AvGrassH). The percent cover of flowering plants was determined by visually estimating the overall coverage at each study site. We used a direct method to measure vegetation height (Stewart *et al*., 2001). In addition five indices were calculated at all study sites using Fragstats 3.3: patch area (AREA), perimeter (PERIM), shape index (SHAPE), fractal dimension index (FRAC) and edge density (ED).

At the landscape scale, we calculated the proportion of the primary land cover types in the area surrounding each study site using ArcGIS 9.3. We used a digital 1:10,000 scale Estonian Basic Map provided by the Estonian Land Board. In the study, we considered five different types of land cover: meadows, forests, young forests (including shrubs, woody seedlings and young trees), arable land and human constructions. All landscape variables were estimated at four spatial scales: 250, 500, 1000 and 2000 m radius. Additionally, five Fragstats indices were calculated: patch richness density (PRD), interspersion and juxtaposition index (IJI), edge density (ED), Shannon's diversity index (SHDI) and the mean patch area of forest (AREA_MN).

Statistical analyses

In the statistical analyses, we used butterfly abundance, calculated as the total number of individuals found in 2008 and 2009 at each meadow, and butterfly species richness, calculated as the total number of species found during the two years, at each meadow. Because total species richness and abundance were strongly correlated, we applied rarefaction to adjust the species richness at different sites to a common number of individuals. We used the total number of species of flowering plants, and the arithmetic mean of percent cover of flowering plants and vegetation height.

The statistical analyses were carried out in various steps. Spearman rank order correlations (STATISTICA 9 software) were used to analyse the relationships between total species richness and abundance of butterflies and between the patch-scale and landscape-scale variables. Additionally, partial least squares (PLS) analysis was performed to simultaneously study the overall butterfly species richness and abundance and different landscape characteristics. Finally, we performed a stepwise forward-selection multiple regression analysis to determine the combinations of the most important predictors for total butterfly species richness and abundance. For each landscape variable, the spatial scale with the strongest relationship was selected, and a significance level of 0.15 was the limit for arguments to remain included in the model. A significance level of 0.15 was used instead of the conventional 0.05 because it was the default limit used by the software and it decreases the chance of omitting potentially significant arguments in the final result during the model building process. The multiple regression analysis and the PLS analysis were performed using SAS 9.1 software.

Results

In total, we recorded 768 individuals belonging to 56 species of butterflies (Appendix). An average of 15.6 species and 34 individuals of butterflies were found per study site. The most abundant butterfly species were *Coenonympha glycerion*, *Aphantopus hyperantus* and *Thymelicus lineola* (with 65, 62 and 61 individuals, respectively). We found 5 species of butterflies that are protected under the EU Habitat Directive Natura 2000: *Parnassius mnemosyne*, *Lycaena dispar*, *Euphydryas maturna*, *Euphydryas aurinia* and *Coenonympha hero*.

Relationships between habitat/landscape characteristics and butterflies

At the patch scale, there were no statistically significant relationships between habitat characteristics and the number of butterfly species, nor abundance.

At the landscape scale, we found that the proportion of forest in the surrounding areas of our study sites was positively correlated with butterfly species richness at 250 m (r_s = 0.428, p = 0.047). The relationships at larger spatial scales were not statistically significant, nor were the correlations between butterfly abundance and forest cover at all landscape scales.

In contrast, we found negative correlations between butterfly species richness/abundance and the proportion of meadows in the surrounding landscape. Statistically significant correlations were found at the spatial scales of 250 m (r_s = -0.514, p = 0.013), 500 m (r_s = -0.544, p = 0.008) and 1000 m (r_s = -0.427, p = 0.047) for species richness and also at 250 m (r_s = -0.508,

p = 0.015), 500 m (r_s = -0.598, p = 0.003) and 1000 m (r_s = -0.512, p = 0.014) for butterfly abundance.

Concerning the relationships between butterflies and other calculated landscape indices, we found no statistically significant relationships except for interspersion and juxtaposition index at 500 m, which was negatively correlated with butterfly species richness (r_s = -0.458, p = 0.032).

Connectivity patterns between butterflies and the local and landscape factors

Two connectivity patterns were identified using PLS analysis, which together accounted for 100% of butterfly richness and abundance variance and 26% of patch and landscape characteristics variance (in Fig. 2, the percentages are presented separately for the two connectivity patterns).

The first connectivity pattern connects the overall number of butterfly species and individuals with the patch and landscape characteristics (first singular vector, Fig. 2). The overall butterfly richness and abundance were significantly and negatively correlated with the proportion of meadows at all spatial scales and with the proportion of arable land at the 250 m spatial scale.

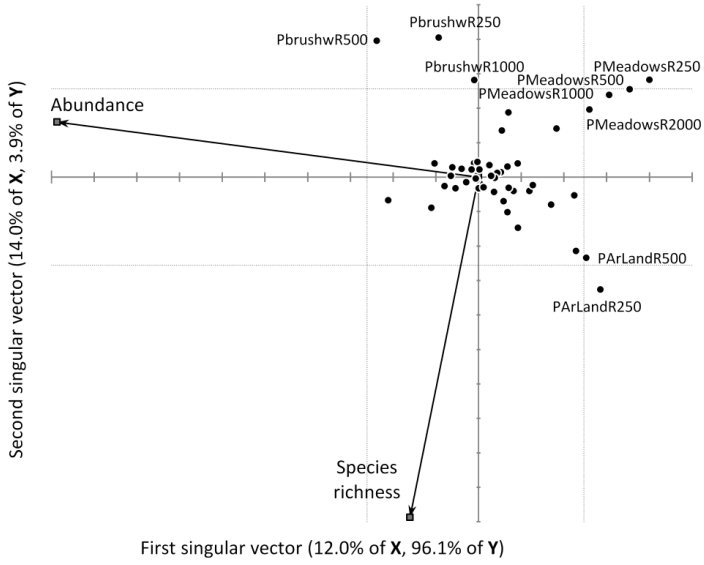

Fig. 2. Results of the partial least squares correlation analyses (PLS) of butterflies. Dots mark the location of patch and landscape characteristics (**X**), and squares with arrows mark the location of the butterfly adjusted richness and abundance (**Y**) in relation to the two latent factors. The patch and landscape characteristics with $p < 0.1$ (as assessed through permutation tests) are presented with the variable name.

The second connectivity pattern (second singular vector, Fig. 2) reflects the changes in relative butterfly species richness (i.e., the heterogeneity/homogeneity of the study sites in relation to the number of individuals). Statistically significant and negative correlations were only found for the second singular vector values corresponding to the proportion of young forest (brushwood) at the spatial scales of 250, 500 and 1000 m. Butterfly species richness may be relatively higher (compared with the number of individuals) if the proportion of young forest is low (especially at the smallest spatial scale) in the surrounding area of the semi-natural meadow patch.

Models to predict butterfly species richness and abundance

The regression models based on the patch and landscape factors tested, explained 68% of the variation in total butterfly abundance and 29% of the species richness (Table 1). The model for total butterfly abundance included five variables: two patch-scale factors and three landscape-scale factors. Species richness of flowering plants was significantly positively related with butterfly abundance and emerged as the most important predictor in our model. All other variables (average cover of flowering plants, patch richness density at the 250 m spatial scale, proportion of meadows and interspersion and juxtaposition index at 500 m) were negatively correlated with total butterfly abundance.

The model for total butterfly species richness included only one landscape-scale factor (Table 1). Adding arguments did not significantly improve the model. The proportion of meadows in the surrounding landscape at the 500 m spatial scale was negatively correlated with total butterfly species richness.

Table 1. Multiple regression models for total butterfly abundance and species richness (adjusted to the common number of individuals).

Dependent variable	R^2 (p-value)	Variable included in the model	Regression coefficient	p-value
Total butterfly abundance	0.68 (0.002)	Species richness of flowering plants (SRFlowPlants)	1.61	<0.001
		Average percent cover of flowering plants (AvCoverFP)	-0.38	0.008
		Proportion of meadows at 500 m (PMeadows R500)	-0.33	0.135
		Patch richness density at 250 m (PRD R250)	-0.39	0.084
		Interspersion and juxtaposition index at 500 (IJI R500)	-1.21	0.005
Total butterfly species richness (adjusted)	0.29 (0.010)	Proportion of meadows at 500 m (PMeadows R500)	-0.04	0.010

Discussion

Effects of patch-scale factors on butterflies

There were no significant relationships between the species richness/abundance of butterflies and flowering plant species richness, the average percent cover of flowering plants and vegetation height. Various factors may be responsible for the absence of these relationships. In general, butterflies are considered to be quite mobile organisms; they usually do not only forage in the patch and, therefore, the floral abundance of the patch is not as important a factor in determining the overall insect species richness and abundance in certain areas. Another possible explanation for butterfly diversity and abundance is that their values might be more influenced by the number and abundance of host plants than total flower abundance (Sjödin *et al*., 2008; Krämer *et al*., 2012).

Other patch-scale factors did also not show significant relationships with butterflies- for example, patch area, which is most frequently found to have a positive effect on butterfly species richness and abundance (Steffan-Dewenter & Tscharntke, 2000; Krauss *et al*., 2003; Brückmann *et al*., 2010; Öckinger *et al*., 2012). The results from this study suggest that butterflies are not only related with a certain patch and its characteristics. Because butterflies are quite mobile, in heterogeneous landscapes, they will use the surrounding landscape for the valuable resources it provides (Dennis, 2004; Bergman *et al*., 2008, Jonason *et al*., 2010). Therefore, for most individual butterfly species, a diverse landscape matrix may comprise all necessary and suitable resources (food, shelter, roosting sites, mating areas, etc.). A number of studies exploring the responses of butterfly species to adjacent habitats have found that butterflies utilise other habitats apart from their main habitat type (Dennis, 2004).

Effects of landscape composition on butterflies

In our study area, the cover of forest habitat significantly influenced butterfly species richness at the smallest landscape scale (radius 250 m). This result indicates that even if butterflies are not directly bounded to the forests as their habitats, they may need forest edges and more mosaic-type landscapes where open landscapes vary with forested landscapes. Additionally, Marini *et al*. (2009) found that the proportion of woody vegetation had the strongest positive effect on butterfly species richness at the local spatial scale and that the significance of forest habitat disappeared as the spatial extent increased. The importance of forest habitat for butterflies is consistent with previous investigations (Kuussaari *et al*., 2007a; Bergman *et al*., 2008; Marini *et al*., 2009, Krämer *et al*., 2012).

There are several possible explanations for the butterfly species' positive response to forest habitat located in the immediate vicinity of their semi-natural habitat patch. First, edge habitats are influenced by environmental conditions characteristic of the adjacent communities and are thereby different from the interior habitats. For example, forest edges have significant gradients of solar radiation, temperature, wind speed and moisture (humidity) between the forest interior and the adjacent meadow habitat. As a result of their diverse microclimate and compositional structure, forest edges may provide such complementary resources as nectar plants for adults and host plants for larvae. Additionally, certain structures may provide suitable sites for female oviposition and the immature stage to accomplish its life cycle (Ouin *et al*., 2004). Several studies have shown that many butterfly species evade open areas such as the patch interior because of the associated higher level of convective cooling, whilst woody vegetation offers shelter against the wind (Kuussaari *et al*., 2007a; Merckx *et*

al., 2008). Furthermore, forest habitat in the close vicinity can serve as a refuge for insects when grasslands are disturbed (Debinski *et al*., 2001; Ouin & Burel, 2002; Marini *et al*., 2009). Because butterfly assemblages consist of species with different habitat requirements, the increased edge density benefits species that require mixed cover types. Linear elements in the landscape also have a positive effect on butterfly diversity (Saarinen *et al*., 2005; Sjödin *et al*., 2008).

In contrast to our expectations, we found that total butterfly species richness and abundance were significantly negatively associated with meadow cover. Furthermore, the model for predicting total butterfly species richness consisted of a single variable- the proportion of meadow at 500 m, which was negatively correlated with butterfly species richness.

The negative influence meadow cover habitat has on butterfly species richness and abundance is related to the positive effect of the forests; meadows as open landscapes are the opposite of forested landscapes. This finding may also be explained by the low suitability of the surrounding meadows for the butterfly species. A decrease in the quality of semi-natural habitats is a result of grassland abandonment and natural afforestation (secondary succession). During the last decade, extensive natural afforestation of semi-natural habitats has occured in Estonia (Kukk & Sammul, 2006) and elsewhere in Europe (Emanuelsson, 2008).

Increasing the proportion of open habitats, such as meadows, causes greater wind speed values. Butterflies in temperate agricultural landscapes prefer sheltered habitats to open habitats (Pywell *et al*., 2004; Kuussaari *et al*., 2007a). The observed negative effect of increasing landscape openness is also in accordance with our results, indicating the positive effect an adjacent forest habitat has on butterfly species richness and abundance.

Additionally, the negative relationship between butterfly species richness and the presence of meadows in the area surrounding the habitat may be related to the composition of butterfly communities and, therefore, differences in resource use. In a forest-dominated landscape, the butterfly community may be composed more of woodland species whose associations with semi-natural meadows (especially small patches between forests) are weak.

Our results support the idea that species communities originate from different landscapes depending on different matrix elements. For example, the amount of semi-natural grasslands in the surrounding landscape may be more important in a landscape dominated by arable fields (Öckinger & Smith, 2007) than in a landscape dominated by forest (Bergman *et al*., 2008). Nevertheless, it should be emphasised that this explanation requires further investigation.

Effects of landscape configuration on butterflies

Butterfly species richness and abundance seem to be negatively influenced by the interspersion and juxtaposition index. Low values of the IJI characterise landscapes in which patch types are distributed disproportionally or clumped together and the greater complexity of the landscape is reflected in an increase in the index (Eiden *et al*., 2000). Because the index shows the complexity of the surrounding habitat and it was negatively related with species richness and the abundance of butterflies, the results show that in our study sites butterflies prefer simplified rather than complex landscapes at the local scale. A possible explanation for this association could be that the studied butterfly communities consist of more generalist species that are not habitat specialists or restricted to certain resources, which means they do

not need additional resources in the form of different patch types. We suggest that the grassland system in forest-dominated landscapes harbours species of butterflies that are specialised to forest-grassland ecotones and mostly depend on the configuration of these land cover types. Finally, we emphasise this as an assumption that needs further investigation. More analyses are needed at the level of individual species and communities in similar landscape patterns.

Conclusions

Our results indicate the importance of the surrounding landscape on butterfly species richness and abundance. Conservation of butterflies should not only focus on preservation of habitat patches. We found that the presence of forest cover in the surrounding landscape has a positive effect on butterfly species richness and abundance. Forest habitats may provide complementary resources for butterflies. Alternately, the vicinity of woody habitat to grassland habitat (especially small meadow patches) harbours certain threats to butterfly species diversity and existence. Such relatively small grassland habitat patches tend to fall out of traditional management regimes and past the processes of natural afforestation (secondary succession), which eventually results in a decrease in quality of these patches for grassland butterflies and will lead to populations of butterflies becoming extinct. Therefore, conservation efforts intended to protect butterflies should be complex, considering interventions both at the patch- and landscape-scale. Consequently, the challenge is to find the landscape heterogeneity level that will support a high diversity of butterfly communities and, therefore, support landscape-based conservation (Dover & Settele, 2009).

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Appendix

List of butterfly species observed in 22 semi-natural meadows in north-eastern Estonia (the nomenclature of the species follows Fauna Europaea).

Hesperiidae

Carterocephalus palaemon
Carterocephalus silvicola
Hesperia comma
Heteropterus morpheus
Ochlodes sylvanus
Pyrgus malvae
Thymelicus lineola
Thymelicus sylvestris

Lycaenidae

Aricia (Plebeius) artaxerxes
Aricia (Plebeius) eumedon
Cupido(Everes) argiades
Cupido(Cupido) minimus
Lycaena alciphron
Lycaena dispar
Lycaena hippothoe
Lycaena phlaeas
Lycaena virgaureae
Plebejus (Plebejus) argus
Plebejus (Plebejus) idas
Polyommatus (Polyommatus) amandus
Polyommatus (Polyommatus) icarus
Polyommatus (Cyaniris) semiargus
Pseudophilotes vicrama

Nymphalidae

Aglais urticae
Aphantopus hyperantus
Araschnia levana
Argynnis (Fabriciana) adippe
Argynnis (Mesoacidalia) aglaja
Argynnis (Argyronome) laodice
Argynnis (Argynnis) paphia
Boloria (Clossiana) selene
Brenthis ino
Coenonympha glycerion
Coenonympha hero
Coenonympha pamphilus
Erebia ligea
Euphydryas aurinia
Euphydryas maturna
Hyponephele lycaon
Inachis io
Lasiommata maera
Lasiommata petropolitana
Maniola jurtina
Melitaea athalia
Melitaea diamina
Polygonia c-album
Vanessa atalanta
Vanessa cardui

Papilionidae

Papilio machaon
Parnassius mnemosyne

Pieridae

Aporia crataegi
Gonepteryx rhamni
Leptidea spp
Pieris brassicae
Pieris napi
Pieris rapae

References

Benton, B.T., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, **18**, 182-188.

Bergman, K.-O., Askling, J., Ekberg, O., Ignell, H., Wahlman, H. & Milberg, P. (2004) Landscape effects on butterfly assemblages in an agricultural region. *Ecography*, **27**, 619–628.

Bergman, K.-O., Ask, L., Askling, J., Ignell, H., Wahlman, H. & Milberg, P. (2008) Importance of boreal grasslands in Sweden for butterfly diversity and effects of local and landscape habitat factors. *Biodiversity and Conservation*, **17**, 139-153.

Brückmann, S.V., Krauss, J. & Steffan-Dewenter, I. (2010) Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. *Journal of Applied Ecology*, **47**, 799-809.

Cozzi, G., Müller, C.B. & Krauss, J. (2008) How do local habitat management and landscape structure at different spatial scale affect fritillary butterfly distribution on fragmented wetlands? *Landscape Ecology*, **23**, 269–283.

Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A. & Wolters, V. (2003) Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agriculture Ecosystems & Environment*, **98**, 321–329.

Davis, J.D., Debinski, D.M. & Danielson, B.J. (2007) Local and landscape effects on the butterfly community in fragmented Midwest USA prairie habitats. *Landscape Ecology*, **22**, 1341–1354.

Debinski, D.M., Ray, C. & Saveraid, E.H. (2001) Species diversity and the scale of the landscape mosaic: do scale of movement and patch size affect diversity? *Biological Conservation*, **98**, 179–190.

Dennis, R.L.H. (2004) Butterfly habitats, broad-scale biotope applications, and structural exploitation of vegetation at finer scales: the matrix revisited. *Ecological Entomology*, **29**, 744–752.

Dover, J. & Settele, J. (2009) The influences of landscape structure on butterfly distribution and movement: a review. *Journal of Insect Conservation*, **13**, 3-27.

Eiden, G., Kayadjanian, M. & Vidal, C. (2000) Capturing landscape structures: Tools. The European Commission. [WWW document]. URL http://ec.europa.eu/agriculture/publi/landscape/ch1.htm. [accessed on 11 March 2013].

Ekroos, J., Heliölä, J. & Kuussaari, M. (2010) Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *Journal of Applied Ecology*, **47**, 459-467.

Emanuelsson, U. (2008) Semi-natural grasslands in Europe today. *Grassland Science in Europe*, **13**, 3-8.

Fahrig, L. (2001) How much habitat is enough? *Biological Conservation*, **100**, 65–74.

Fauna Europaea (2012) Fauna Europaea version 2.5. [WWW document]. URL http://www.faunaeur.org [accessed on 22 January 2012].

Jonason, D., Milberg, P. & Bergman, K-O. (2010) Monitoring of butterflies within a landscape context in south-eastern Sweden. *Journal for Nature Conservation*, **18**, 22-33.

Krauss, J., Steffan-Dewenter, I. & Tscharntke, T. (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography*, **30**, 889–900.

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K.M., Sang, A., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2010) Habitat

fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters*, **13**, 597-605.

Krämer, B., Poniatowski, D. & Fartmann, T. (2012) Effects of landscape and habitat quality on butterfly communities in pre-alpine calcareous grasslands. *Biological Conservation*, **152**, 253-261.

Kukk, T. & Sammul, M. (2006) Area of seminatural Natura 2000 habitat types in Estonia. *Year-book of the Estonian Naturalists' Society*, **84**, 114–159.

Kumar, S., Simonson, S.E. & Stohlgren, T.J. (2009) Effects of spatial heterogeneity on butterfy species richness in Rocky Mountain National Park, CO, USA. *Biodiversity and Conservation*, **18**, 739–763.

Kuussaari, M., Heliölä, J., Luoto, M. & Pöyry, J. (2007a) Determinants of local species richness of diurnal Lepidoptera in boreal agricultural landscapes. *Agriculture Ecosystems & Environment*, **122**, 366-376.

Kuussaari, M., Heliölä, J., Pöyry, J. & Saarinen, K. (2007b) Contrasting trends of butterfly species preferring semi-natural grasslands, field margins and forest edges in northern Europe. *Journal of Insect Conservation*, **11**, 351-366.

Luoto, M., Rekolainen, S., Aakkula, J. & Pykälä, J. (2003) Loss of plant species richness and habitat connectivity in grasslands associated with agricultural change in Finland. *Ambio*, **32**, 447–452.

Maes, D., Titeux, N., Hortal, J., Anselin, A., Decleer, K., De Knijf, G., Fichefet, V. & Luoto, M. (2010) Predicted insect diversity declines under climate change in an already impoverished region. *Journal of Insect Conservation*, **14**, 485-498.

Marini, L., Fontana, P., Battisti, A. & Gaston, K.J. (2009) Agricultural management, vegetation traits and landscape drive orthopteran and butterfly diversity in a grassland–forest mosaic: a multi-scale approach. *Insect Conservation and Diversity*, **2**, 213-220.

Merckx, T., Van Dongen, S., Matthysen, E. & Van Dyck, H. (2008) Thermal flight budget of a woodland butterfly in woodland versus agricultural landscapes: An experimental assessment. *Basic and Applied Ecology*, **9**, 433-442.

Mortelliti, A., Amori, G. & Boitani, L. (2010) The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. *Oecologia*, **163**, 535-547.

Ouin, A., Aviron, S., Dover, J. & Burel, F. (2004) Complementation/supplementation of resources for butterflies in agricultural landscapes. *Agriculture Ecosystems & Environment*, **103**, 473–479.

Ouin, A. & Burel, F. (2002) Influence of herbaceous elements on butterfly diversity in hedgerow agricultural landscapes. *Agriculture Ecosystems & Environment*, **93**, 45–53.

Öckinger, E. & Smith, H.G. (2006) Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. *Oecologia*, **149**, 526–534.

Öckinger, E. & Smith, H.G. (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, **44**, 50–59.

Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Pöyry, J., Settele, J., Summerville, K.S. & Bommarco, R. (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecology Letters*, **13**, 969-979.

Öckinger, E., Lindborg, R., Sjödin, N.E. & Bommarco, R. (2012) Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography*, **35**, 259–267.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637-669.

Pöyry, J., Luoto, M., Hekkinen, R.K., Kuussaari, M & Saarinen, K. (2009) Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, **15**, 732-743.

Pywell, R.F., Warman, E.A., Sparks, T.H., Greatorex-Davies, J.N., Walker, K.J., Meek, W.R., Carvell, C., Petit, S. & Firbank, L.G. (2004) Assessing habitat quality for butterflies on intensively managed arable farmland. *Biological Conservation*, **118**, 313–325.

Rossi, J.-P. & van Halder, I. (2010) Towards indicators of butterfly biodiversity based on a multiscale landscape description. *Ecological Indicators*, **10**, 452-458.

Saarinen, K., Valtonen, A., Jantunen, J. & Saarnio, S. (2005) Butterflies and diurnal moths along road verges: Does road type affect diversity and abundance? *Biological Conservation*, **123**, 403–412.

Shreeve, T.G. & Dennis, R.L.H. (2011) Landscape scale conservation: resources, behaviour, the matrix and opportunities. *Journal of Insect Conservation*, **15**, 178-188.

Sjödin, N.E., Bengtsson, J. & Ekbom, B. (2008) The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. *Journal of Applied Ecology*, **45**, 763-772.

Steffan-Dewenter, I. & Tscharntke, T. (2000) Butterfly community structure in fragmented habitats. *Ecology Letters*, **3**, 449-456.

Stewart, K.E.J., Bourn, N.A.D. & Thomas, J.A. (2001) An evaluation of three quick methods commonly used to assess sward height in ecology. *Journal of Applied Ecology*, **38**, 1148-1154.

Stoate, C., Boatman, N.D., Borrahlon, R.J., Carvalho, C.R., de Snoo, G.R. & Eden, P. (2002) Ecological impacts of arable intensification in Europe. *Journal of Environmental Management*, **63**, 337–365.

Thomas, J.A., Bourn, N.A.D., Clarke, R.T., Stewart, K.E., Simcox, D.J., Pearman, G.S., Curtis, R. & Goodger, B. (2001) The quality and isolation of habitat patches both determine where butterfies persist in fragmented landscapes. *Proceedings of the Royal Society B-Biological Sciences*, **268**, 1791–1796.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, **8**, 857-874.

van Swaay, C., Warren, M. & Lois, G. (2006) Biotope use and trends of European butterflies. *Journal of Insect Conservation*, **10**, 189–209.

van Swaay, C.A.M., van Strien, A.J., Harpke, A., Fontaine, B., Stefanescu, C., Roy, D., Maes, D., Kühn, E., Õunap, E., Regan, E., Švitra, G., Prokofev, I., Heliölä, J., Settele, J., Pettersson, L., Botham, L., Musche, M., Titeux, N., Cornish, N., Leopold, P., Julliard, R., Verovnik, R., Öberg, S., Popov, S., Collins, S., Goloshchapova, S., Roth, T., Brereton, T. & Warren, M. (2013) The European Grassland Butterfly Indicator: 1990-2011. European Environment Agency, Copenhagen, Denmark.

Weibull, A.-C. & Östman, Ö. (2003) Species composition in agroecosystems: The effect of landscape, habitat, and farm management. *Basic and Applied Ecology*, **4**, 349-361.

III

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INFLUENCE OF LOCAL AND LANDSCAPE FACTORS ON BUMBLEBEES IN SEMI-NATURAL MEADOWS: A MULTIPLE-SCALE STUDY IN A FORESTED LANDSCAPE
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ORIGINAL PAPER

Influence of local and landscape factors on bumblebees in semi-natural meadows: a multiple-scale study in a forested landscape

Isabel Diaz-Forero · Valdo Kuusemets · Marika Mänd · Ave Liivamägi · Tanel Kaart · Jaan Luig

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Abstract Understanding the effects of local and landscape factors on bumblebees is relevant for the conservation of this group of pollinators. Bumblebees have been well-studied in agricultural landscapes of Western Europe, Asia and North America, but few studies have been developed on bumblebees in forest-dominated landscapes of Eastern Europe. We developed this study in 22 semi-natural meadows located in a patchy forested landscape of Estonia. We investigated the influence of habitat characteristics and landscape factors (calculated at four spatial scales: 250, 500, 1,000 and 2,000 m radius) on the total species richness and abundance of bumblebees. Correlation analysis, partial least squares (PLS) and stepwise forward-selection multiple regression analysis were applied in this study. The presence of a high diversity of flowering plants in semi-natural meadows may benefit the abundance of bumblebees. At the local level, patch area and shape seem to have positive and negative influences, respectively, on bumblebee species richness. At the landscape level, human settlements with the presence of gardens may favour bumblebee richness and abundance. Also, bumblebee species may increase with a high presence of meadows in the landscape, and may decrease with high percentages of forest and young forest. Overall, forested landscapes with a strong presence of edges and a diverse matrix may support a higher species richness and abundance of bumblebees. Both local and landscape factors should be considered when designing conservation strategies and agri-environmental measures.

Keywords *Bombus* · Land cover types · Landscape indices · Fragstats · Partial least squares (PLS) · Landscape matrix

I. Diaz-Forero (✉) · V. Kuusemets · M. Mänd · A. Liivamägi · J. Luig
Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5, 51014 Tartu, Estonia
e-mail: isadiazf@gmail.com; isabel.diaz@emu.ee

T. Kaart
Institute of Veterinary Medicine and Animal Sciences, Estonian University of Life Sciences, Kreutzwaldi 62, 51014 Tartu, Estonia

Introduction

In recent decades, the decline of insect pollinators, particularly bees, has been widely recognised. Evidence of this decline has been documented across the world and in several European countries (Kells and Goulson 2003; Samways 2005; Williams and Osborne 2009; Potts et al. 2010). Bumblebees and other insects are a vital component of global biodiversity as they play a key role in supporting not only crops, but also the diversity of natural and semi-natural vegetation (Sepp et al. 2004; Goulson et al. 2006; Rundlöf et al. 2008; Ahrné et al. 2009; Knight et al. 2009; Potts et al. 2010; Goulson et al. 2011). Their decline has been mainly associated with agricultural intensification that is characterised by the rigorous use of fertilisers and pesticides and the reduction of flower resources (Carvell 2002; Mänd et al. 2002; Goulson et al. 2006; Holzschuh et al. 2008; Xie et al. 2008; Ahrné et al. 2009); causing the fragmentation of landscapes and the loss of suitable habitats for insects (Krewenka et al. 2011). Agri-environmental schemes are being applied in many European countries to alleviate the negative consequences of the intensification of farming practices on biodiversity. The development of more effective agri-environmental measures has become an issue of great concern among decision makers, mainly due

to the growing interest of politicians, farmers and consumers in more environmentally-friendly farming practices (Kleijn et al. 2006; Holzschuh et al. 2008).

Bumblebees have been well-studied in modern agricultural landscapes of Western Europe, the United Kingdom, Japan and North America (Goulson et al. 2011). However, very little is known about the distribution, conservation and ecology of bumblebees elsewhere (Goulson et al. 2011). Those areas that have been well-studied usually consist of large monoculture fields separated by field margins and few patches of woodland. In contrast, the landscape in Estonia has a very mosaic pattern, where 32 % of the whole territory is agricultural land, but only a small proportion is cultivated, and it contains many patches of natural habitat (Mänd et al. 2002). Moreover, there is evidence that the proportion of forest in Estonia increased substantially during the twentieth century (from 14 to 42 %) (Palang et al. 1998). Understanding the associations between bumblebees and the surrounding landscape is relevant for the conservation of this group of pollinators, particularly in areas that have fragmented landscapes with high proportions of forest and natural habitats. Generally, bumblebees have been studied in regions with warmer climates (compared to Estonia) and open landscapes, mostly in agricultural landscapes (e.g., Steffan-Dewenter 2003; Hatfield and LeBuhn 2007; Krewenka et al. 2011). Therefore, research on bumblebee populations conducted on the northern regions and in more forested landscapes are of great interest. To our knowledge, very few studies have been developed on the influence of landscape factors on bumblebees in forested landscapes.

Most conservation strategies for pollinators have focused on habitat characteristics and requirements of species at the local level, excluding the potential effects of the surrounding landscape mosaic (Steffan-Dewenter et al. 2002; Cozzi et al. 2008). However, the effectiveness of biodiversity conservation usually depends on the knowledge about the influence of different factors at multiple scales on the distribution of organisms and the conditions that allow them to move across the landscape (Gutzwiller 2002).

In our study, we considered patch and landscape factors that may have potential relevance to the ecology of bumblebee species richness and abundance; some of them have been used in previous studies on insects (e.g., Mazerolle and Villard 1999; Krauss et al. 2003; Kumar et al. 2009). Patch can be defined as "a relatively homogeneous area that differs from its surroundings" (Freemark et al. 2002). For the purposes of this study, patch-scale refers to local-scale: so when talking about patch-scale variables, it means the characteristics or factors at the scale of the habitat or meadow under study. Our landscape variables were chosen considering a set of principles for applying landscape ecology to biological conservation, suggested by Freemark et al. (2002). The first one is to "maintain landscape mosaics that are more permeable" (Freemark et al. 2002); in this case we chose variables related with connectivity or with aspects that may influence the dispersal patterns of species (e.g., interspersion and juxtaposition index, edge density). The second one is to "maintain landscape mosaics with sufficient proportion of suitable habitat" (Freemark et al. 2002); in our study we considered the proportion of important land cover types in the surrounding landscape (e.g., meadows, forest, young forest). The third principle is: "with sufficient suitable habitat, patch size distribution is of secondary importance" (Freemark et al. 2002); concerning this principle, we included factors related with the distribution and configuration of individual patches (e.g., mean patch area of forest), and with the configuration of the landscape matrix (e.g., Shannon's diversity index). From an ecological perspective, what comprises a landscape will generally depend on the scales over which a given species moves and its perception of the surroundings (Manning et al. 2004); that is, the relevant scale of a landscape depends on the organism, or the ecological process under study (Freemark et al. 2002). In the case of bumblebees, we considered four spatial scales (i.e., 250, 500, 1,000 and 2,000 m radius) taking into account the ranges of flight distances of different bumblebee species: as it was reported in a recent study, some species can flight more than 2 km (Hagen et al. 2011).

Considering that Estonia has a patchy landscape with a relevant presence of natural and semi-natural land cover types (mainly forest), the aim of this study was to investigate the influence of patch-scale and landscape-scale factors on the species richness and abundance of bumblebees. At the local level (or patch scale), we considered variables describing the vegetation structure and other spatial characteristics of the study sites (e.g., patch area, perimeter and shape). At the landscape level, we used the proportion of the most important land cover types in the study region (i.e., forests, meadows, young forest, arable land and human settlements) and a set of landscape indices that were calculated at multiple spatial scales.

Materials and methods

Study area

The study was carried out in Ida-Virumaa, which is located in northeast Estonia (Fig. 1). This region is affected mainly by mining activities as it contains large deposits of oil shale, the mineral used for power generation in Estonia. The study was conducted in 22 semi-natural meadows that differ in vegetation characteristics, size and shape, and in their

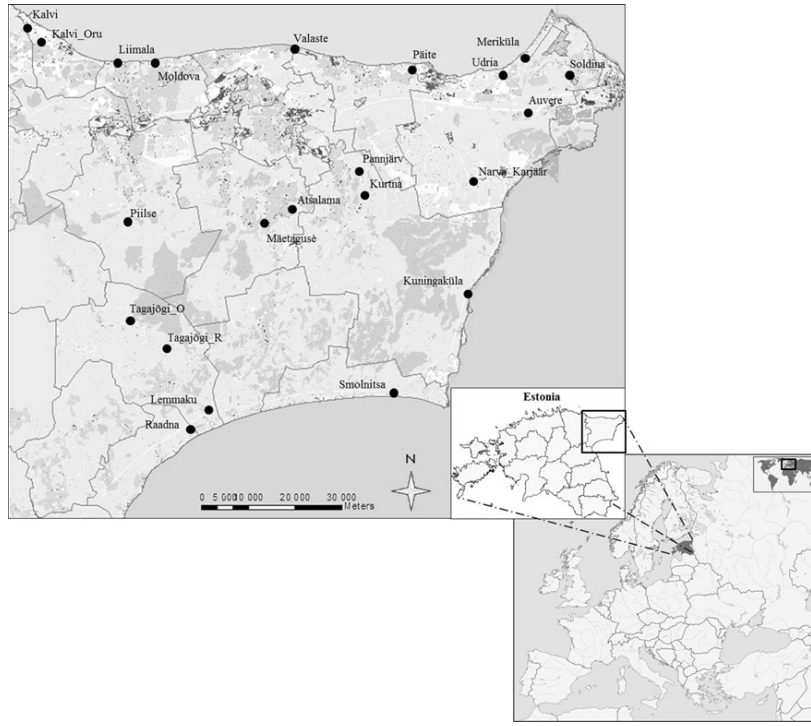

Fig. 1 Map of the study region, Ida-Virumaa County, Estonia, with the location of the 22 study sites

surrounding landscape composition and configuration. The areas of the selected meadows ranged from 0.10 to 3.83 ha.

The study region is characterised by a patchy landscape structure with a variety of land cover types, predominantly forest (195,245 ha, approximately 58.0 % of the territory in the region), arable land (41,671 ha, approximately 12.4 %), young forest (21,701 ha, approximately 6.5 %) and meadows (19,031 ha, approximately 5.7 %), and smaller proportions of human settlements, mires, green areas, etc. The forest cover in the region is mainly composed of managed mixed forest; birches, pines and spruces are among the dominant trees. The total area of our study region is 336,400 ha, which represents about 7.4 % of the total area of Estonia (the territory of Estonia occupies 45,000 km^2, Peterson and Aunap 1998). The population density in the region is about 50 inhabitants per km^2 (Statistics Estonia 2012).

Bumblebee survey

The fieldwork was carried out during the summers of 2008 and 2009. Every year, we sampled each meadow twice: first during June, and second between the end of July and the beginning of August. The recordings were made via systematic walking surveys. Bumblebee counts were conducted during the warmer time of the day, between 10:00 and 16:00 h, under suitable weather conditions, in which the temperature was above 18 °C and the wind speed was less than five on the Beaufort scale. Our fieldwork method was based on Goulson et al. (2006). Each visit was done during a period of about 45 min to 1 h, or until the observer was satisfied that all the species on the site were recorded. The species richness and abundance of bumblebees was determined by counting individuals and identifying species by sight, mainly when they were visiting flowers. When the observer could not identify the bumblebee species on site,

some individuals were caught with an insect net for later identification in the laboratory. The nomenclature used was based on Fauna Europaea (2011).

Variables at the patch scale

At each study site, we recorded variables that described the structure of the vegetation. Specifically, we registered the number of species of flowering plants, the percent cover of flowering plants and the grass height at the end of each visit. The percent cover of flowering plants was determined through a visual estimation of the overall coverage and was performed by the same person at all study sites. We used a direct method to measure grass height (Stewart et al. 2001). The "direct measurement method" consists of placing a hand lightly on the vegetation at the level below which about 80 % of the vegetation is estimated by eye to be growing, ignoring occasional tall stalks, and then reading the height with the help of a rule (Stewart et al. 2001). In the statistical analyses, we used the total number of species of flowering plants recorded in the first year, and the arithmetic mean of the four observations (one per visit) of percent cover of flowering plants and grass height. The cover of flowering plants was measured in percentages with an accuracy of 10 %.

In addition, five indices were calculated at all study sites with Fragstats (Version 3.3): area (AREA), perimeter (PERIM), shape index (SHAPE), fractal dimension index (FRAC) and edge density (ED). SHAPE characterises the complexity of a patch shape compared to a standard shape. In this study, the raster version of Fragstats was used, which evaluates patch shape with a square standard; this means that shape index is minimum for square patches and increases as patches become increasingly non-square (or more irregular) (McGarigal and Marks 1995). Shape index is commonly applicable and has been widely used in landscape ecological research (Forman and Godron 1986). FRAC is another measure of shape complexity (McGarigal and Marks 1995), but it is calculated based on the patch size. Fractal is defined as a geometric form that displays structure at all spatial scales (McGarigal and Marks 1995). To calculate the fractal dimension of natural planar shapes, he proposed a perimeter-area method. This method quantifies the degree of complexity of the planar shapes (McGarigal and Marks 1995). On the other hand, ED (or alternatively Perimeter Area Ratio—PAR) at the patch level is a function of the patch perimeter and it takes into account the shape and the complexity of the patch (McGarigal and Marks 1995).

Variables at the landscape scale

To analyse the composition of the landscape, the proportion of the main land cover types in the area surrounding each study site was calculated using ArcGIS 9.3. We used a digital Estonian Basic Map provided by the Estonian Land Board at the scale of 1:10,000. The original maps included more than 30 different land cover types that were organised into 11 categories: meadows, forest, young forest (successional young forest that has been growing after clear cutting or on abandoned land. It includes shrubs, woody seedlings and young trees), mires, arable land, abandoned peatland, bodies of fresh water, sea, green areas, human settlements (including residential areas, private areas, buildings, cattle sheds, roads, ruins and green houses) and others. After calculating the percentage of each land cover type at four spatial scales (i.e., 250, 500, 1,000 and 2,000 m radius), we chose only the most relevant land cover types, those that had the strongest presence in the study region (i.e., the land cover types than occupy more than 5 % of the territory) ("Appendix 1"): forest, arable land, young forest (also called "brushwood"), meadows and human settlements.

We used five Fragstats indices to describe the configuration of the landscape (Fragtats, version 3.3) ("Appendix 1"): patch richness density (PRD), interspersion and juxtaposition index (IJI), edge density (ED), Shannon's diversity index (SHDI) and mean patch area of forest (AREA_MN). These indices were chosen because they describe important aspects of the landscape structure and may influence bumblebee species richness and abundance. PRD was used to standardize patch richness to a per area basis (McGarigal and Marks 1995). We used IJI to measure the extent to which patch types are interspersed (not necessarily dispersed); higher values are given to landscapes in which the patch types are well interspersed (or equally adjacent to each other), whereas lower values are given to landscapes in which the patch types are poorly interspersed (or the distribution of patch type adjacencies is disproportionate) (McGarigal and Marks 1995). Interspersion can be defined as "the degree to which a given patch or landscape type is scattered rather than aggregated or crumpled", and juxtaposition is the "adjacency of different patch or landscape types" (Freemark et al. 2002). ED_LAND equals the length of all borders between different patch types (classes) in a reference area divided by the total area of the reference unit; in contrast to patch density, edge density takes the shape and the complexity of the patches into account (Eiden et al. 2000). Edge density measures the complexity of the shapes of patches and, similar to patch density is an expression of the spatial heterogeneity of a landscape mosaic (Eiden et al. 2000). Additionally, SHDI was used to measure the diversity of the landscape based on two components: richness, defined as the number of different patch types, and evenness in the distribution of areas among patch types (Eiden et al. 2000). Finally, we used AREA_MN to describe the distribution and configuration of patches of the most predominant land

cover type in the study region: forest. AREA_MN equals the sum, across all patches of the corresponding patch type (here, forest) of the area of the patches, divided by the total number of patches of the same type (McGarigal et al. 2002). We used "mean patch size" because it gives information about the size of the patches and the number of patches at the same time.

Statistical analyses

In the statistical analyses, we used the total bumblebee abundance calculated as the total number of individuals found in 2008 and 2009, and the total bumblebee species richness calculated as the total number of species found during the 2 years at each study site. Before performing the analyses, the logarithm and square root transformations were applied to the bumblebee variables (bumblebee species richness and abundance) and landscape parameters, respectively, to normalise the data. As the total bumblebee species richness and abundance were strongly correlated, we applied the rarefaction to adjust the species richness at different sites to the common number of individuals.

The statistical analyses were developed in various steps. First, we conducted Spearman rank order correlations to analyse the relationships between the total species richness and abundance of bumblebees, and the patch-scale and landscape-scale factors (for a description of the variables, see "Appendix 1"). When the correlation coefficient (r_s) was between 0.0 and ± 0.3, the correlation was considered weak; when r_s was between ± 0.3 and ± 0.6, the correlation was medium; and when r_s was between ± 0.6 and ± 1, the correlation was strong; in all cases, the correlation was statistically significant if the p value was less than 0.05. Second, to simultaneously examine the connectivity patterns of the patch and landscape characteristics, and the overall bumblebee species richness and abundance the partial least squares (PLS) analysis was applied. PLS is the multivariate statistical technique particularly well suited for situations where multicollinearity exists in the dataset and the number of variables is high compared to the number of observations (about PLS in ecological studies, see Carrascal et al. 2009, for example). In this study, the connectivity patterns (called also latent factors) of two centred and normalized bumblebee variables stored in matrix $\mathbf{Y}$ (i.e., adjusted total bumblebee species richness and total number of individuals), and 50 centered and normalized patch and landscape characteristics (i.e., 10 patch-scale variables and 40 landscape-scale variables) stored in matrix $\mathbf{X}$ were evaluated by singular value composition of the form $\mathbf{Y'X} = \mathbf{USV'}$ (apostrophe denotes the matrix transposition). Matrixes $\mathbf{U}$ and $\mathbf{V}$ are the matrixes of the left and right singular vectors (representing the bumblebee richness and abundance profiles and landscape profiles, respectively), best characterizing the correlation between $\mathbf{X}$ and $\mathbf{Y}$; matrix $\mathbf{S}$ contains the singular values measuring the quality of latent factors (for a detailed description of PLS, see Krishnan et al. 2011). The percent of variation accounted for by partial least squares factor i was evaluated as the ratio of the sums of squares of latent variables and initial variables: $R^2_{Xi} = \mathrm{SS}(\mathbf{XV}_i)/\mathrm{SS}(\mathbf{X})$ and $R^2_{Yi} = \mathrm{SS}(\mathbf{YU}_i)/\mathrm{SS}(\mathbf{Y})$ for landscape characteristics and bumblebee richness and abundance, respectively; $\mathbf{V}_i$ and $\mathbf{U}_i$ denote the ith column of the matrix. To test the statistical significance of latent factors the permutation test with 10,000 permutation samples was applied (to correct for the axis rotations and reflections the Procrustes rotation was used). This permutation also served to assess the singular vectors, giving a threshold to decide which variables were contributing the most of the latent factor.

Finally, we performed the stepwise forward-selection multiple regression analysis to determine the combinations of the most important predictors for total bumblebee species richness and abundance. For each landscape variable, the spatial scale with the strongest relationship was selected and the significance level 0.15 was the limit for arguments to stay in the model. The significance level 0.15, instead of the conventional 0.05, was used as it was the default limit used by the software and it decreases the chance to drop out arguments potentially significant in the final result during the model building process.

We used STATISTICA 9 software to perform the correlation analyses. The multiple regression analysis and the PLS analysis were performed with SAS 9.1 software.

Results

Bumblebee species richness and abundance

We identified 19 species of bumblebees (gen. *Bombus*) and 5 species of cuckoo bumblebees (gen. *Bombus*, Subgen. *Psithyrus*) in the study area ("Appendix 2"). They represent approximately 83 % of the total bumblebee species found in Estonia. Currently in the country there are 29 species of bumblebees, including 7 species of cuckoo bumblebees. An average of 10.7 species and 27.1 individuals of bumblebees were found per study site. The total number of individuals recorded was 597, including 150 males, 84 queens and 363 workers. The most abundant species were *B. pascuorum*, *B. lucorum* and *B. ruderarius* with 140, 70 and 58 individuals in total, respectively. In contrast, *B. muscorum* and *B. distinguendus* were the species with the lowest abundance.

As it was mentioned before, total bumblebee species richness was strongly positively correlated with total bumblebee abundance ($r_s = 0.94$, $p < 0.001$); however, after

rarefaction was applied to adjust bumblebee species richness to the common number of individuals, this relationship was weak and not significant ($r_s = 0.27, p = 0.233$).

Relations between patch-scale factors and bumblebees

A total of 133 species of flowering plants were found in our study sites. Flowering plant species richness ranged from 7 to 43 species per study site. We found that bumblebee abundance was strongly positively correlated with flowering plant species richness ($r_s = 0.65, p < 0.001$).

Concerning the relations between the spatial characteristics of the meadows and bumblebees, we found that bumblebee species richness was strongly negatively correlated with shape index (SHAPE) ($r_s = -0.60$, $p = 0.003$) and medium negatively correlated with fractal dimension index (FRAC) ($r_s = -0.57$, $p = 0.004$). There were not significant relationships neither between bumblebees and other spatial characteristics, nor between bumblebees and average grass height or average percent cover of flowering plants ($p > 0.05$).

Relations between landscape-scale factors and bumblebees

We found that the proportion of human settlements in the areas surrounding our study sites was positively correlated with bumblebee abundance at 250 and 1,000 m ($r_s = 0.48$, $p = 0.024$; $r_s = 0.51$, $p = 0.014$, respectively). Additionally, bumblebee species richness was positively correlated with the proportion of meadows at the largest spatial scale, i.e., 2,000 m ($r_s = 0.51$, $p = 0.015$). Concerning the relations between bumblebees and landscape indices, we found positive correlations between bumblebee abundance and Shannon's diversity index (SHDI) at 2,000 m and edge density (ED_LAND) at 1000 m ($r_s = 0.44$, $p = 0.039$; $r_s = 0.50$, $p = 0.018$, respectively).

In contrast, we found that proportion of forest was negatively correlated with bumblebee species richness at the spatial scales of 1,000 and 2,000 m ($r_s = -0.45$, $p = 0.036$; $r_s = -0.47$, $p = 0.025$, respectively). Also, negative correlations were detected between proportion of young forest and bumblebee species richness at 250 and 500 m ($r_s = -0.57$, $p = 0.005$; $r_s = -0.44$, $p = 0.040$, respectively). Mean patch area of forest at the largest spatial scale was also negatively correlated with bumblebee species richness ($r_s = -0.51$, $p = 0.015$).

Connectivity patterns between bumblebees and the local and landscape factors

Two connectivity patterns were identified with partial least squares (PLS) analysis, which together accounted for 100 and 31.5 % of bumblebee richness and abundance variance, and patch and landscape characteristics variance, respectively (in Fig. 2, the percentages are presented separately for the two connectivity patterns).

The first connectivity pattern connects mainly the overall number of species and individuals of bumblebees with the patch and landscape characteristics (First singular vector, Fig. 2). According to the permutation test, the overall bumblebee richness and abundance were significantly positively related with the proportion of human settlements, especially at the smallest spatial scale ($p < 0.05$). In contrast, the proportion of arable land at the scale of 250 m, the proportion of young forest also at 250 m and mean patch area of forests (AREA_MN) (especially at larger spatial scales) showed negative relations ($p < 0.05$) with the bumblebee richness and abundance pattern, indicating that the larger the values of these variables, the smaller the number of species and individuals of bumblebees.

The second connectivity pattern (Second singular vector, Fig. 2) reflects the changes in relative bumblebee species richness (i.e., how heterogeneous or homogeneous are the study sites in relation to the number of individuals). Statistically significant were only the second singular vector values corresponding to the proportion of arable

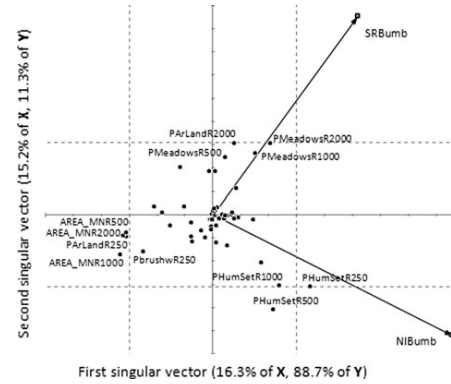

Fig. 2 Results of the partial least squares (PLS) analysis. The dots mark the location of the patch and landscape characteristics (**X**) and the squares with arrows mark the location of the bumblebee species richness (adjusted) and abundance (**Y**) in relation to the two connectivity patterns. The *dotted lines* denote the approximate cut-off for statistical significance of the right singular vectors (patch and landscape characteristics vectors) as assessed through permutation tests ($p = 0.05$); for clearness only the patch and landscape characteristics with $p < 0.1$ are shown with the variable name. R250, R500, R1000 and R2000, denote the different spatial scales at which the landscape factors were calculated. (The abbreviations are explained in the "Appendix 1")

Table 1 Regression models for total bumblebee abundance and total bumblebee species richness (adjusted to the common number of individuals)

Dependent variable	R^2	Variable included in the model	Regression coefficient	*p* value
Total bumblebee abundance	0.83*	Species richness of flowering plants	0.44	<0.001
		Proportion of arable land at 250 m	−0.08	0.008
		Mean patch area of forest (AREA_MN) at 1,000 m	−0.12	0.048
		Edge density at landscape level (ED_Land) at 1,000 m	0.09	0.120
Total bumblebee species richness (adjusted)	0.73*	Patch area (AREA)	0.18	0.028
		Shape index (SHAPE)	−0.88	0.003
		Proportion of arable land at 2,000 m	−0.05	0.025
		Mean patch area of forest (AREA_MN) at 1,000 m	−0.16	<0.001
		Patch richness density (PRD) at 500 m	−0.13	0.103

* Significant at $p < 0.001$

land at the spatial scale of 2,000 m, proportion of meadows also at the largest spatial scale, and proportion of human settlements at 1,000 m ($p < 0.05$). The second singular vector values of proportion of arable land and proportion of meadows were positive, which mean that the relative species richness of bumblebees may be higher (compared with the number of individuals) if the proportion of arable land and meadows is high (particularly at the largest spatial scale). The negative second singular vector values of proportion of human settlements indicate that the relative species richness may be lower (compared with the number of individuals) if the proportion of human settlement is high (especially at the smallest spatial scale).

Models to predict bumblebee species richness and abundance

The regression models based on the patch and landscape factors tested here explained 83 and 73 % of the variation in total bumblebee abundance and species richness, respectively (Table 1). Both models were highly statistically significant. The model for total bumblebee abundance included four variables: one patch-scale factor and three landscape-scale factors. Species richness of flowering plants was significantly positively related with bumblebee abundance and emerged as the most important predictor in our model. In contrast, two landscape variables, proportion of arable land and mean patch area of forest (AREA_MN), were negatively related with bumblebee abundance.

Five variables were included in the model for total bumblebee species richness: two patch-scale factors and three landscape-scale factors (Table 1). The most important predictor of bumblebee species richness was shape index (SHAPE). Patch area (AREA) was significantly positively related with bumblebee richness, whereas SHAPE, proportion of arable land and AREA_MN were all negatively related with the dependant variable.

Discussion

Effects of patch-scale factors on bumblebees

This study shows that the diversity of flowering plants is a very important factor for total bumblebee abundance. Similarly, Rundlöf et al. (2008) found that local abundance of forage resources was significantly positively associated with bumblebee abundance, but not with bumblebee species richness. Also, they found that higher abundance of flowering plants was associated with higher abundance of bumblebees from large colonies (Rundlöf et al. 2008). The number of individuals of bumblebees may depend on the availability of flowering resources, because generally the most common and abundant species tend to be those that have a broad diet and emerge early in the season (Goulson et al. 2005), whereas specialist species (e.g., some long-tongued bumblebees) are less abundant as they often depend on a small number of plant species (Goulson and Darvill 2004; Goulson et al. 2005; Goulson 2010). In general, our results indicate that enhancing the presence of flowering plant species in semi-natural meadows may increase the abundance of bumblebees. This result is consistent with previous studies, which have suggested that the species richness of flowering plants is an important local factor for bumblebee communities (e.g., Bäckman and Tiainen 2002; Mänd et al. 2002; Kells and Goulson 2003; Hatfield and LeBuhn 2007; Rundlöf et al. 2008; Ahrné et al. 2009).

Patch area seems to have a positive influence on bumblebee species richness. This makes sense as the larger the

area of the habitat, the higher the chances of finding the suitable food resources and nesting sites that bumblebee species require. Also, in patches of smaller size, habitat-specialist plants may have a higher probability of extinction (Quintana-Ascencio and Menges 1996); this may influence some bumblebee species that depend on these types of plants. Previous studies on insects have also found significant positive relationships between habitat area and species richness (Steffan-Dewenter and Tscharntke 2000; Krauss et al. 2003; Steffan-Dewenter 2003; Öckinger and Smith 2006).

Other patch-scale factors, specifically shape index and fractal dimension index, showed negative relationships with bumblebee species richness. Shape index was also one of the main predictors of bumblebee species richness. This index describes the complexity of the patch shape; this means that the more irregular the shape of the habitat, the lower may be the number of species in that habitat. The importance of patch shape on organisms can be described using the "interior-to-edge ratio" (Forman and Godron 1986): a circular or square patch consists mostly of an interior area with a surrounding band of edge. A square patch has a higher "interior-to-edge ratio" compared to a patch with a more complex or irregular shape (with the same area), as the latest has proportionally less interior area. Forman and Godron (1986) suggested that patches with higher "interior-to-edge ratio" may have higher species diversity, less probability of presence of barriers within the patch, and more foraging efficiency for animals inside the patch. However, the effect of patch shape on the foraging efficiency has not been well studied and further research is needed. The fractal dimension index is also related with the shape of the patch; it is another measure of shape complexity, but it is calculated based on the patch size.

Effects of landscape composition on bumblebees

We found that bumblebee abundance was positively influenced by the proportion of human settlements at various spatial scales. However, population density in this region is rather low (about 50 inhabitants/sq km) and approximately 81.5 % of the population is living in the cities (Statistics Estonia 2012). Overall bumblebee richness and abundance was also positively related with the proportion of human settlements (in the first connectivity pattern, in PLS), particularly at the smallest spatial scale. This may be explained by the presence of gardens in residential areas, which may support a high diversity of flowering plants and thus provide suitable nesting sites, shelter and alternative foraging resources for bumblebees. This has been found also in previous studies in the case of bees in general (Cussans et al. 2010), and particularly bumblebees (Goulson et al. 2002; McFrederick and LeBuhn 2006; Goulson et al. 2010). Some abundant bumblebee species, such as *B. ruderarius*, seem to prefer plant communities close to human settlements (Söderman 1999). Generally, people like to have plants with blossoms in their gardens, so the percentage of nectar-rich flowers might be high in human-inhabited areas. Gardens seem to support extraordinarily high densities of nests for bumblebees (Osborne et al. 2008; Goulson 2010).

In contrast, Ahrné et al. (2009) found that the proportion of urban areas had a negative effect on bumblebee richness, as the increased presence of urban structures such as roads and buildings decreases the proportion of suitable habitat patches for bumblebees, such as field boundaries and pastures. However, most of our study sites were located relatively far from large towns, which mean that the density of roads, especially main roads, is very low, and the presence of buildings and houses is not very evident. Also, the roadsides and field boundaries in Estonia are commonly covered by lush herbaceous flora (Mänd et al. 2002), which may favour bumblebees. Our measurements of the proportion of human settlements included also the presence of abandoned buildings (ruins) or gardens with ruderal plants; these areas are very common in Estonia and may offer places with a high diversity of flowering plants. In addition, Winfree et al. (2007) suggested that bee species richness may be higher when the proportion of natural habitats in the landscape is high, even though the level of human disturbance is intermediate; that is, the negative effects of human disturbance may occur only when the proportion of natural land cover is very low. Our study region is cover by high proportions of forests, young forest and meadows; this means that the presence of these land cover types may mask the effect of human settlements on bumblebees.

Our results show that bumblebee species richness may increase with the presence of meadows in the landscape at the largest spatial scale. Similarly, Hatfield and LeBuhn (2007) found that the most consistent positive influence on species richness of bumblebees was the proportion of meadows in the surrounding landscape, at a 2-km buffer from the edge of the focal habitat. In addition, Le Féon et al. (2010) found that the species richness, abundance and diversity of bees were negatively affected by agricultural intensification, whereas bee species richness was positively affected by the amount of semi-natural habitats in the landscape. On the other hand, it has been found that, in general, bumblebees have large foraging ranges (Steffan-Dewenter et al. 2002; Westphal et al. 2006; Hatfield and LeBuhn 2007); some species are known to fly more than 2,000 m (e.g., *B. pascuorum* and *B. terrestris*) (Chapman et al. 2003; Zurbuchen et al. 2010). Dispersal abilities of bumblebees allow them to retrieve floral resources in adjacent meadows; increasing the probability of finding the

flowering plants that some species require (Hatfield and LeBuhn 2007).

Bumblebee species richness seems to be negatively influenced by the presence of forest in the surrounding landscape at the largest spatial scales. This may happen because some bumblebee species may not be able to find their suitable nesting sites in the forest and also, they may have different preferences in terms of the landscape context. Goulson (2010) suggested that the sites chosen for nesting vary between species, depending on the habitat type and the place where this habitat is located. Also, overall bumblebee species richness appears to be negatively influenced by the proportion of young forest. These areas are commonly dominated by willows that often grow in wetlands and along the forest edges (Sepp et al. 2004). These habitats are rich in blooming flowers and are important for bumblebees in early spring (i.e., April and May), particularly for some species that emerge early in the season. Many patches of young forest have grown in areas that were former meadows; the soil in these areas is rich in calcium and can therefore support a great amount of flowering plant species. However, areas dominated by willows may also represent an ecological trap for bumblebees: early emerging species might tend to build their nests near the forest, where later in the season food would become scarce and these areas would no longer be able to provide enough forage resources for bumblebees.

On the other hand, bumblebee species richness and abundance were negatively associated with the proportion of arable land. The negative effect of arable land on bumblebees may be explained by the openness of the landscape in those areas, which could make the bumblebees more vulnerable to wind and other climatic factors, as there are fewer places that may offer shelter and protection. Also, foraging resources are sometimes scarce in agricultural land and this may result in the decline of bumblebees (Goulson et al. 2005), while the presence of semi-natural grasslands in the landscape context may increase the presence of bumblebees (Öckinger and Smith 2007). Grasslands are more likely to contain a higher availability of nests for bumblebees than the surrounding cultivated land (Öckinger and Smith 2007). Similarly, Le Féon et al. (2010) found in a recent study that bee species richness and abundance were negatively affected by agricultural intensification. Overall pollinator diversity may be enhanced by the presence of semi-natural habitats in the landscape context (Jauker et al. 2009; Le Féon et al. 2010).

Effects of landscape configuration on bumblebees

Bumblebee abundance seems to be positively influenced by edge density at landscape level. This positive relation may occur because there is a strong dependency of bumblebee abundance on the availability of flowering plants (as it was mentioned above). Kumar et al. (2009) explained that habitat edges contain a great abundance and diversity of floral resources, making them suitable places for flower visitors. The presence of edges and other compensating areas nearby the main habitat is very important to bumblebees' survival, as they may find complementary food resources and nesting places there. Furthermore, bumblebee queens are more frequently observed along forest boundaries and field boundaries (Svensson et al. 2000). Similarly, Sepp et al. (2004) found that the distribution of bumblebees was positively related with the length of ecotones between cultivated land and different types of forest. A study on bumblebees in Estonia suggested that edges are particularly important in April and May, when bumblebee queens mostly forage the flowering willows that are commonly found in the forest edges (Sepp et al. 2004). Positive effects of linear elements, such as edges, on bumblebees have been found before (Osborne et al. 2008).

We found that Shannon's diversity index seems to be an important landscape metric for bumblebee abundance at the largest spatial scale. This index indicates the complexity of the surrounding landscape matrix, and increases as the number of different patch types increases and the distribution of patch types becomes more equitable (Eiden et al. 2000). This means that our study sites are surrounded by different patch types that might be suitable habitat fragments for bumblebees, increasing the availability of food resources in the landscape and thus, their likelihood of survival. Other authors have found similar positive relationships between insects and the diversity of the landscape matrix (e.g., Steffan-Dewenter 2003; Kivinen et al. 2006). Kivinen et al. (2006) argued that in boreal agricultural landscapes, the presence of patches of semi-natural grasslands and other non-crop biotopes in adjacent open areas may have a positive effect on the species richness of some insects (such as butterflies), as movement of species between different habitat types can increase overall species richness in the landscape context.

In contrast, overall bumblebee species richness and abundance appear to be negatively influenced by mean patch area of forest. A possible explanation for this negative association may be that a high number of patches of forest could be seen as potential obstacles in the landscape by some species of foraging bumblebees (Kreyer et al. 2004; Goulson et al. 2010), particularly for those species that have large foraging distances, such as *B. lapidarius* and *B. terrestris* (Walther-Hellwig and Frankl 2000a, b). Similarly, Winfree et al. (2007) found that bee species richness and abundance were negatively associated with the extent of forest cover, suggesting that the number of bees decreased as forest cover increased in the surrounding landscape.

Conclusions and implications for conservation

We found that not only the availability of food resources at patch level, but also the quality and diversity of the surrounding landscape, are important factors affecting bumblebee species richness and abundance.

The results from this study have important implications for the conservation of bumblebees and for the development of agri-environmental measures in patchy forested landscapes. First, the presence of a high diversity and abundance of flowering plants may benefit bumblebee abundance in semi-natural meadows, but considering only local factors may not be sufficient. Second, the existence of edges in patchy forested landscapes may support bumblebees, as these are considered compensating areas that may offer shelter, food and protection for them. Third, the presence of human settlements in the landscape matrix may favour bumblebees, particularly when these areas include gardens and other places with a high diversity of flowering plants, and when the percentage of natural and semi-natural habitats in the landscape is high, particularly meadows. Finally, bumblebees benefit from a rich and diverse landscape matrix with an important presence of patches of natural and semi-natural habitats.

Policies supporting agri-environmental measures should be improved, because if financial resources target only one farmer or only changes at the local level, these measures are not likely to be very effective for biodiversity conservation. Changes at the level of one farm are not sufficient to support the entire system that also incorporates the surrounding landscape. To maintain biodiversity, heterogeneous landscapes including patches of semi-natural habitats need to be preserved. In conclusion, we should consider not only variables at the local level but also the landscape context around targeted areas at large spatial scales when designing conservation strategies for bumblebees and agri-environmental measures.

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Appendix 1

See Table 2.

Table 2 Local and landscape variables considered in this study

Variable	Description	Unit
Bumblebees		
SRBumb	Bumblebee species richness; number of species	–
NIBumb	Bumblebee abundance; number of individuals	–
Vegetation structure at local level		
SRFlowPlants	Species richness of flowering plants; number of species	–
AvCoverFP	Average percent cover of flowering plants. Percentage of the meadow that is covered by flowering plants	%
AvGrassH	Average grass height	cm
Spatial characteristics at local level (Fragstats indices)		
AREA	Patch area; size of the patch	ha
PERIM	Perimeter of the patch	m
SHAPE	Shape index; SHAPE equals patch perimeter (m) divided by the square root of patch area (m^2), adjusted by a constant to adjust for a circular standard (vector) or square standard (raster)[a]	–
FRAC	Fractal dimension index; FRAC equals 2 times the logarithm of patch perimeter (m) divided by the logarithm of patch area (m^2)[a]	–
ED	Edge density; sum of the length (m) of the edge segment of the patch per unit area[a]	m/ha
Landscape composition		
Pforest	Proportion of patches that are forests	%
Pmeadows	Proportion of patches that are meadows	%
PArLand	Proportion of patches that are arable land	%
PHumSet	Proportion of patches that are human settlements; including residential areas, buildings, cattle sheds, roads, ruins (or buildings' remains) and green houses	%

Table 2 continued

Variable	Description	Unit
Pbrushw	Proportion of patches that are young forests (also called "brushwood"); it includes shrubs, woody seedlings and young trees	%
Landscape configuration (Fragstats indices)		
PRD	Patch richness density; PRD equals the number of patch types per 100 ha[a]	No/100 ha
IJI	Interspersion and juxtaposition index; measure of distribution of patch adjacencies[a]	%
ED_LAND	Edge density at landscape level; total length of all edge segments per unit area of landscape[a]	m/ha
SHDI	Shannon's diversity index; SHDI equals minus the sum, across all patch types, of the proportional abundance of each patch type multiplied by that proportion[a]	–
AREA_MN	Mean patch area of forests; AREA_MN equals the sum, across all patches of the corresponding patch type, in our case forest, of the area of the patches, divided by the total number of patches of the same type[a]	ha

[a] *Source*: McGarigal et al. (2002)

Appendix 2

See Table 3.

Table 3 List of bumblebee species (gen. *Bombus*) and the number of individuals found

Bumblebee species	Number of individuals
Bombus cryptarum (Fabr.)	24
Bombus distinguendus Morawitz	1
Bombus hortorum (L.)	11
Bombus hypnorum (L.)	9
Bombus jonellus (Kirby)	18
Bombus lapidarius (L.)	26
Bombus lucorum (L.)	70
Bombus muscorum (L.)	1
Bombus pascuorum (Scopoli)	140
Bombus pratorum (L.)	15
Bombus ruderarius (Müller)	58
Bombus semenoviellus Skorikov	7
Bombus schrencki Morawitz	16
Bombus soroeensis ssp. *Soroeensis* (Fabr.)	14
Bombus soroeensis ssp. *Proteus* (Fabr.)	16
Bombus soroeensis ssp. *soroeensis x proteus* (Fabr.)	21
Bombus sylvarum (L.)	18
Bombus terrestris (L.)	18
Bombus veteranus (Fabr.)	27
Bombus bohemicus Seidl.	33
Bombus campestris (Panzer)	16
Bombus norvegicus (Sparre-Schneider)	11
Bombus rupestris (Fabr.)	18
Bombus sylvestris (Lep.)	9

References

Ahrné K, Bengtsson J, Elmqvist T (2009) Bumble bees (*bombus* spp) along a gradient of increasing urbanization. PLoS ONE 4:e5574

Bäckman JP, Tiainen J (2002) Habitat quality of filed margins in a Finnish farmland area for bumblebees (Hymenoptera: *Bombus* and *Psithyrus*). Agr Ecosyst Environ 89:53–68

Carrascal LM, Galván I, Gordo O (2009) Partial least squares regression as an alternative to current regression methods used in ecology. Oikos 118:681–690

Carvell C (2002) Habitat use and conservation of bumblebees (*Bombus* spp) under different grassland management regimes. Biol Conserv 103:33–49

Chapman RE, Wang J, Bourke AFG (2003) Genetic analysis of spatial foraging patterns and resource sharing in bumble bee pollinators. Mol Ecol 12:2801–2808

Cozzi G, Müller CB, Krauss J (2008) How do local habitat management and landscape structure at different spatial scales affect fritillary butterfly distribution on fragmented wetlands? Landscape Ecol 23:269–283

Cussans J, Goulson D, Sanderson R, Goffe L, Darvill B, Osborne JL (2010) Two bee-pollinated plant species show higher seed production when grown in gardens compared to arable farmland. PLoS ONE 5:e11753

Eiden G, Kayadjanian M, Vidal C (2000) Capturing landscape structures: Tools. The European Commission. http://ec.europa.eu/agriculture/publi/landscape/ch1.htm. Accessed 10 Oct 2011

Fauna Europaea (2011) Fauna Europaea version 2.4. http://www.faunaeur.org. Accessed 15 June 2011

Forman RTT, Godron M (1986) Landscape ecology. Wiley, New York

Freemark K, Bert D, Villard MA (2002) Patch-, landscape-, and regional-scale effects on biota. In: Gutzwiller KJ (ed) Applying landscape ecology in biological conservation. Springer, New York, pp 58–83

Goulson D (2010) Bumblebees: behaviour, ecology and conservation. Oxford University Press, Oxford

Goulson D, Darvill B (2004) Niche overlap and diet breadth in bumblebees; are rare species more specialized in their choice of flowers? Apidologie 35:55–64

Goulson D, Hughes WHO, Derwent LC, Stout JC (2002) Colony growth of the bumblebee, *Bombus terrestris*, in improved and

conventional agricultural and suburban habitats. Oecologia 130: 267–273
Goulson D, Hanley ME, Darvill B, Ellis JS, Knight ME (2005) Causes of rarity in bumblebees. Biol Conserv 122:1–8
Goulson D, Hanley ME, Darvill B, Ellis JS (2006) Biotope associations and the decline of bumblebees (*Bombus* spp). J Insect Conserv 10:95–103
Goulson D, Lepais O, O'Connor S, Osborne JL, Sanderson LA, Cussans J, Goffe L, Darvill B (2010) Effects of land use at a landscape scale on bumblebee nest density and survival. J Appl Ecol 47:1207–1215
Goulson D, Rayner P, Dawson B, Darvill B (2011) Translating research into action; bumblebee conservation as a case study. J Appl Ecol 48:3–8
Gutzwiller KJ (2002) Spatial factors affecting organism occurrence, movement, and conservation: introduction to section II. In: Gutzwiller KJ (ed) Applying landscape ecology in biological conservation. Springer, New York, pp 55–57
Hagen M, Wikelski M, Kissling WD (2011) Space use of bumblebees (*Bombus* spp) revealed by radio tracking. PLoS ONE 6(5):e19997
Hatfield RG, LeBuhn G (2007) Patch and landscape factors shape community assemblage of bumble bees, *Bombus* spp. (Hymenoptera: Apidae), in montane meadows. Biol Conserv 139:150–158
Holzschuh A, Steffan-Dewenter I, Tscharntke T (2008) Agricultural landscapes with organic crops support higher pollinator diversity. Oikos 117:354–361
Jauker F, Diekötter T, Schwarzbach F, Wolters V (2009) Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landscape Ecol 24:547–555
Kells AR, Goulson D (2003) Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. Biol Conserv 109:165–174
Kivinen S, Luoto M, Kuussaari M, Helenius J (2006) Multi-species richness of boreal agricultural landscapes: effects of climate, biotope, soil and geographical location. J Biogeogr 33:862–875
Kleijn D, Baquero RA, Clough Y et al (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecol Lett 9:243–254
Knight ME, Osborne JL, Sanderson RA, Hale RJ, Martin AP, Goulson D (2009) Bumblebee nest density and the scale of available forage in arable landscapes. Insect Conserv Divers 2:116–124
Krauss J, Steffan-Dewenter I, Tscharntke T (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? J Biogeogr 30:889–900
Krewenka KM, Holzschuh A, Tscharntke T, Dormann CF (2011) Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. Biol Conserv 144:1816–1825
Kreyer D, Oed A, Walther-Hellwig K, Frankl R (2004) Are forests potential landscape barriers for foraging bumblebees? Landscape scale experiments with *Bombus terrestris* agg and *Bombus pascuorum* (Hymenoptera, Apidae). Biol Conserv 116(1):111–118
Krishnan A, Williams LJ, McIntosh AR, Abdi H (2011) Partial least squares (PLS) methods for neuroimaging: a tutorial and review. NeuroImage 56:455–475
Kumar S, Simonson SE, Stohlgren TJ (2009) Effects of spatial heterogeneity on butterfly species richness in Rocky Mountain National Park, CO, USA. Biodivers Conserv 18:739–763
Le Féon V, Schermann-Legionneta A, Delettrea Y et al (2010) Intensification of agriculture, landscape composition and wild bee communities: a large scale study in four European countries. Agr Ecosyst Environ 137:143–150
Mänd M, Mänd R, Williams IH (2002) Bumblebees in the agricultural landscape of Estonia. Agr Ecosyst Environ 89:69–76
Manning AD, Lindenmayer DB, Nix HA (2004) Continua and Umwelt: alternative ways of viewing landscapes. Oikos 104:621–628
Mazerolle MJ, Villard MA (1999) Patch characteristics and landscape context as predictors of species presence and abundance: a review. Ecoscience 6:117–124
McFrederick QS, LeBuhn G (2006) Are urban parks refuges for bumble bees *Bombus* spp (Hymenoptera: Apidae)? Biol Conserv 129:372–382
McGarigal K, Marks BJ (1995) FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Gen. Tech. Rep. PNW-GTR-351 Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station
McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS, spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst
Öckinger E, Smith HG (2006) Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. Oecologia 149:526–534
Öckinger E, Smith HG (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. J Appl Ecol 44:50–59
Osborne JL, Martin AP, Shortall CR, Todd AD, Goulson D, Knight ME, Hale RJ, Sanderson RA (2008) Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. J Appl Ecol 45:784–792
Palang H, Mander Ü, Luud A (1998) Landscape diversity changes in Estonia. Landsc Urban Plan 41:163–169
Peterson U, Aunap R (1998) Changes in agricultural land use in Estonia in the 1990s detected with multitemporal Landsat MSS imagery. Landsc Urban Plan 41:193–201
Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25:345–353
Quintana-Ascencio PF, Menges ES (1996) Inferring metapopulation dynamics from patch-level incidence of Florida of scrub plants. Conserv Biol 10(4):1210–1219
Rundlöf M, Nilsson H, Smith HG (2008) Interacting effects of farming practice and landscape context on bumble bees. Biol Conserv 141:417–426
Samways MJ (2005) Insect diversity conservation. Cambridge University Press, New York
Sepp K, Mikk M, Mänd M, Truu J (2004) Bumblebee communities as an indicator for landscape monitoring in the agri-environmental programme. Landsc Urban Plan 67:173–183
Söderman G (1999) Diversity of pollinator communities in Eastern Fennoscandia and Eastern Baltics results from pilot monitoring with yellow traps in 1997–1998. Finnish Environment Institute. Edita Ltd, Helsinki
Statistics Estonia (2012) Statistical database: population by county in 2009. http://www.stat.ee. Accessed 1 April 2012
Steffan-Dewenter I (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Conserv Biol 17:1036–1044
Steffan-Dewenter I, Tscharntke T (2000) Butterfly community structure in fragmented habitats. Ecol Lett 3:449–456
Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tscharntke T (2002) Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83:1421–1432
Stewart KEJ, Bourn NAD, Thomas JA (2001) An evaluation of three quick methods commonly used to assess sward height in ecology. J Appl Ecol 38:1148–1154
Svensson B, Langerlöf J, Svensson BG (2000) Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. Agr Ecosyst Environ 77:247–255
Walther-Hellwig K, Frankl R (2000a) Foraging habitats and foraging distances of bumblebees, *Bombus* spp (Hym, apidae), in an agricultural landscape. J Appl Entomol 124:299–306

Walther-Hellwig K, Frankl R (2000b) Foraging distances of *Bombus muscorum*, *Bombus lapidarius*, and *Bombus terrestris* (Hymenoptera, Apidae). J Insect Behav 13(2):239–246

Westphal C, Steffan-Dewenter I, Tscharntke T (2006) Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. Oecologia 149:289–300

Williams PH, Osborne JL (2009) Bumblebee vulnerability and conservation world-wide. Apidologie 40:367–387

Winfree R, Griswold T, Kremen C (2007) Effect of human disturbance on bee communities in a forested ecosystem. Conserv Biol 21: 213–223

Xie Z, Williams PH, Tang Y (2008) The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan. J Insect Conserv 12:695–703

Zurbuchen A, Landert L, Klaiber J, Muller A, Hein S, Dorn S (2010) Maximum foraging ranges in solitary bees: only a few individuals have the capability to cover long foraging distances. Biol Conserv 143:669–676

IV

Liivamägi, A., Kuusemets, V., Luig, J. & Kask, K. 2013
CHANGES IN THE DISTRIBUTION OF CLOUDED APOLLO *PARNASSIUS MNEMOSYNE* (LEPIDOPTERA: PAPILIONODAE) IN ESTONIA.
Entomologica Fennica 24 (3): 186-192

Changes in the distribution of Clouded Apollo *Parnassius mnemosyne* (Lepidoptera: Papilionidae) in Estonia

Ave Liivamägi, Valdo Kuusemets, Jaan Luig & Kadri Kask

Liivamägi, A., Kuusemets, V., Luig, J. & Kask, K. 2013: Changes in the distribution of Clouded Apollo *Parnassius mnemosyne* (Lepidoptera: Papilionidae) in Estonia. — Entomol. Fennica 24: 186–192.

Clouded Apollo (*Parnassius mnemosyne*) has been occupying three separate areas in Estonia and has increased its abundance and population area remarkably during the last 30 years. Since the butterfly was first identified in the northeast (1878) and southeast (1984) of Estonia, the species has expanded its distribution with overall expansion distances of approximately 135 and 100 km, respectively. In western Estonia, the butterfly was found locally on the island of Saaremaa in 1922–1973. Today, the butterfly is most likely extinct there. The occupational trend of the species in Estonia is not in accordance with its general trend in Europe, where it has shown a continuous decline. We suggest that in Estonia there is a suitable landscape structure with the presence of suitable landscape elements and still enough semi-natural grasslands that are suitable habitats for the butterfly even despite the fact that the traditional extensive agricultural practice in general is decreasing in Estonia.

A. Liivamägi, V. Kuusemets, J. Luig & K. Kask, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5, Tartu, 51014, Estonia; Corresponding author's e-mail: ave.liivamagi@emu.ee

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1. Introduction

Many European butterfly species are endangered, and their distribution has declined during recent decades (Van Swaay *et al.* 2010). One widely distributed and endangered specialist species that has received much attention over recent decades and that has been well studied by several researchers (Konvička & Kuras 1999, Meglécz *et al.* 1999, Luoto *et al.* 2001, Välimäki & Itämies 2003, Meier *et al.* 2005, Gratton *et al.* 2008, Gorbach & Kabanen 2010) is Clouded Apollo, *Parnassius mnemosyne* (Linnaeus 1758). Over the entire distribution range, this Palaearctic species has discrete populations. In Northern Europe, the species occurs in flat semi-natural grasslands (Luoto *et al.* 2001, Meier *et al.* 2005), but in Central Europe, it is found in forest steppes, sparse deciduous forests and forest clearings (Konvička & Kuras 1999).

The distribution and abundance of Clouded Apollo has declined in North Europe, e.g. Finland (Väisänen & Somerma 1985), Sweden (Bergström 2005), Norway (Aagaard & Hansen 1992), and in Central Europe (Konvička & Kuras 1999). However, there are few studies providing evidence in which *P. mnemosyne* has increased its abundance and expanded its distribution area (see Gorbach & Kabanen 2010).

Due to the vulnerability of the populations of Clouded Apollo and due to several reports about local extinctions or the limited distribution of

populations (Bergström 2005), the species is protected in Europe by the Bern Convention, the EU Habitat Directive Natura 2000 (CEE Habitat Directive 43/92, annex IV), and national protection acts, and it is included in many regional Red Data Books. In Estonia, the butterfly has been under legal protection since 1995.

Clouded Apollo has been occupying three geographically separate areas in Estonia: west, northeast and southeast. In accordance with a regional separation, three subspecies have been described: *P. mnemosyne osiliensis* (Bryk 1922) in Saaremaa Island; *P. mnemosyne estonicus* (Viidalepp 2000) in north-eastern Estonia, and *P. mnemosyne viidaleppi* (Kesküla & Luig 1997) in south-eastern Estonia. The first record of *P. mnemosyne* in north-eastern Estonia was in 1878. In 1922 the butterfly was discovered on the island of Saaremaa and in 1984 in southern part of Estonia. The last information of the existence of the species on the island of Saaremaa is from 1973. During the same year, 2 individuals were caught and 30 were reported to be seen (Kesküla 1989). There are no later records from the area, despite that many entomologists have searched for the butterfly. The subspecies is probably extinct today. In two other parts of Estonia, Clouded Apollo has expanded its distribution.

The geographical distribution of Clouded Apollo is generally related to the distribution of its host plants and to certain environmental conditions required by the given species. The larva of the species is monophagous on the plant genus *Corydalis*. In Estonia, they mainly feed on the leaves of *C. solida*. Therefore, the distribution of Clouded Apollo depends on the distribution of its larval host plant species.

The other general factors that make a biotope suitable for Clouded Apollo are food resources for adults, suitable habitat patches and surrounding landscape structure. Due to the specific requirements of environmental and habitat conditions, populations of Clouded Apollo are in danger of becoming fragmented, which may lead to the extinction of the butterfly. Therefore, it is important to study the state and distribution changes of Clouded Apollo in different parts of its distribution.

The aim of this study was to examine the abundance and distribution changes of Clouded Apollo in Estonia during the period of 1878–2010. Understanding the pattern of the distribution and abundance of the butterfly is necessary for planning effective conservation of the species.

2. Material and methods

We collected and organised all known records of the findings of Clouded Apollo in Estonia to a database. The database includes data from various sources, such as literature, insect collections, records from researchers and local surveys of the butterfly. Whereas the purpose of the studies and the collections of the butterfly have differed and have been performed by different groups of people (amateur lepidopterists, qualified lepidopterists, volunteers), there are several duplications of records and variation in the accuracy of data.

Most of the earlier records were more general, describing the name of the place or the description of the location using landmark features such as roads, rivers, trees and bushes, some of the data were described within a 10 x10 km UTM square. The accuracy of these data was several kilometres but at least 5 km.

The records from years 1981–2010 were taken from the national periodical review called LepInfo (a publication of the Estonian Lepidopterologists' Society and the Section for entomology of the Estonian Naturalists' Society that collects all findings of most butterfly species in Estonia). The accuracy of these records is generally better than in the case of older data, because all records are fixed according to the coordinates of the Estonian national grid system (10 × 10 km) and concurrently international UTM grid system. During the last ten years, records of the butterfly (and the exact position of the habitat patch) have been additionally collected by the authors of this paper using portable GPS units.

The accuracy differs among separate data sets but in all it is adequate for analysing the species distribution for the scale of the whole Estonian during the long time period (132 years) since the first record of Clouded Apollo in Estonia.

All descriptions of the findings of the butterfly were linked on a digital cadastral map of Estonia (1:10,000) to the common GIS database using MapInfo Professional 9.0. The database of

Table 1. Summary of records of *Parnassius mnemosyne* in Estonia.

Study periods	Regions	No. of findings per region	No. of sites per region	No. of individuals per site
1878–1969	NE	32	8	1–44
	W	9	1	1–20
	SE	–	–	–
1970–1979	NE	12	6	1–17
	W	1	1	–
	SE	–	–	–
1980–1989	NE	19	11	1–37
	W	–	–	–
	SE	13	9	1–9
1990–1999	NE	14	11	1–50
	W	–	–	–
	SE	81	42	1–200
2000–2010	NE	57	48	1–60
	W	–	–	–
	SE	69	44	1–300

Clouded Apollo consists of data about the exact location of the findings (place name or coordinates if possible), class of accuracy on a 1–3 scale (1: exact location, 2: grid system coordinates, 3: descriptive location), date and time of the observation, name of the observer, gender and the number of individuals if determined and counted, source of data and a short description of the habitat. For analyses of the distribution changes we divided our data into five study periods: 1878–1969, 1970–1979, 1980–1989, 1990–1999 and 2000–2010. The first period is longer than the rest, because there were only single records of the butterfly from this period.

Finally, for the general evaluation of the relations between the distribution of the butterfly and its larval food plant *Corydalis solida*, the distribution map of the plant species in Estonia was derived from the Atlas of the Estonian Flora where the data are displayed in a grid of 9 × 11 km squares (Kukk & Kull 2005).

3. Results

There are 307 records of Clouded Apollo in Estonia from the period 1878–2010. Of the five study periods, most records of distribution (82%) are from 1980 and later. Only 18% of all records are from the period 1878–1979.

During the first study period 1878–1969, there are 41 records of Clouded Apollo, with the majority of them located in eight places in north-eastern Estonia and only one location (Kübassaare) on the island of Saaremaa (Table 1). During the period 1970–1979, there are 13 records with the majority of them located in north-eastern Estonia and one on the island of Saaremaa. During these two study periods the number of individuals of *P. mnemosyne* seen at the sites of findings varied between 1–44. During the period 1980–1989, there are 32 records in Estonia. The butterfly was registered 19 times in north-eastern and 13 times in south-eastern Estonia. Number of individuals varied between 1 and 37. During the period 1990–1999 and 2000–2010, there are 95 and 126 records of *P. mnemosyne*, respectively. Approximately two thirds of the findings from the last two study periods are locating in south-eastern Estonia where the number of recorded individuals has reached 300.

Changes in the distribution trends of Clouded Apollo in Estonia are shown in Fig. 1. During the period 1878–1969, the distribution of the butter-

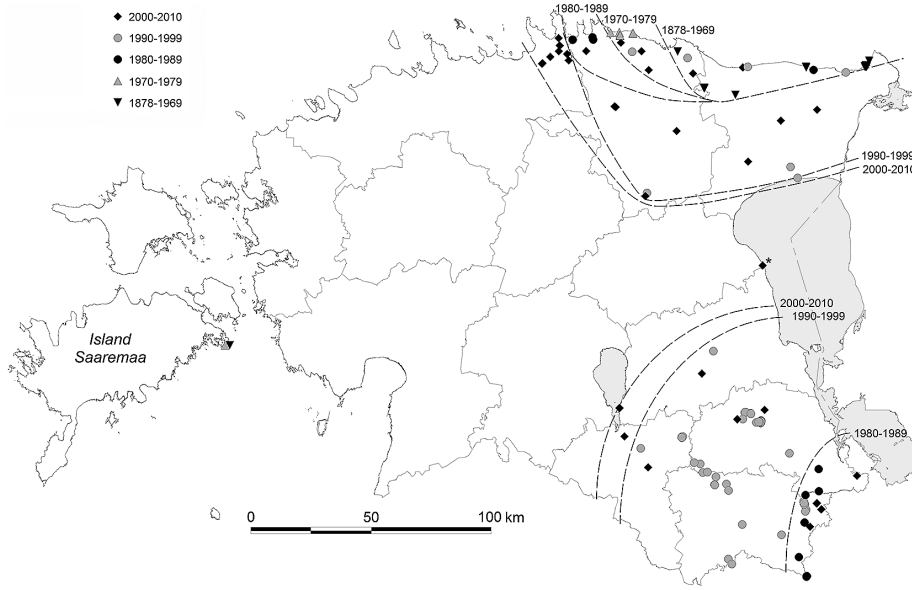

Fig. 1. Distribution of Clouded Apollo (*Parnassius mnemosyne*) in Estonia in 1878–2010. Broken lines show the extent of the butterfly distribution in a given period. The record with an asterisk (*) concerns a single instance from the year 2002 (5 individuals) with no records there later. Therefore, the 2000–2010 line was not drawn to include this record.

fly remained local in north-eastern Estonia. During the periods 1970–1979 and 1980–1989, the species moved westward, with decennial maximum expansion distances of approximately 30 km and 20 km, respectively (Fig. 1). During the last two decades (1990–1999, 2000–2010) the expansion of the butterfly has continued to the west and to the south. In contrast, on the island of Saaremaa the butterfly was found during the period 1922–1973 but it remained local and few in numbers in its habitats over the entire period.

Until the middle of the 1980s, Clouded Apollo was found only in north-eastern Estonia and on the island of Saaremaa. In southern Estonia the butterfly was first recorded in 1984 near to the rivers Pedetsi and Piusa. Six years later, the butterfly was already found approximately 40 kilometres to the north in the Ahja River catchment and five years later approximately 35 kilometres to the northwest in the Võhandu River catchment. A more substantial increase, 30 to 50 km in occupancy to the north and north-westerly directions, was observed in the period 1990–2000.

The distribution pattern of Clouded Apollo in Estonia and that of its larval host plant *Corydalis solida* are generally consistent (Figs 1 and 2). *Corydalis solida* is mainly growing in northern and south-eastern part of Estonia and in some areas on islands. The plant is almost missing in the central part of Estonia. Only in north-western part there are areas with *C. solida* but no findings of Clouded Apollo.

4. Discussion

The data sets used in our study differed in quality, but we consider their precision adequate for analysing the distributional changes of *P. mnemosyne* in the scale of whole Estonia during the long time period. However, one can suspect more representative recording effort in the recent data than in the older ones. We concur that recent recording tends to be more systematic and organised. On the other hand, entomologists had been visiting similar habitats suitable for *P. mnemosyne* also in earlier years, and a rare butterfly species has re-

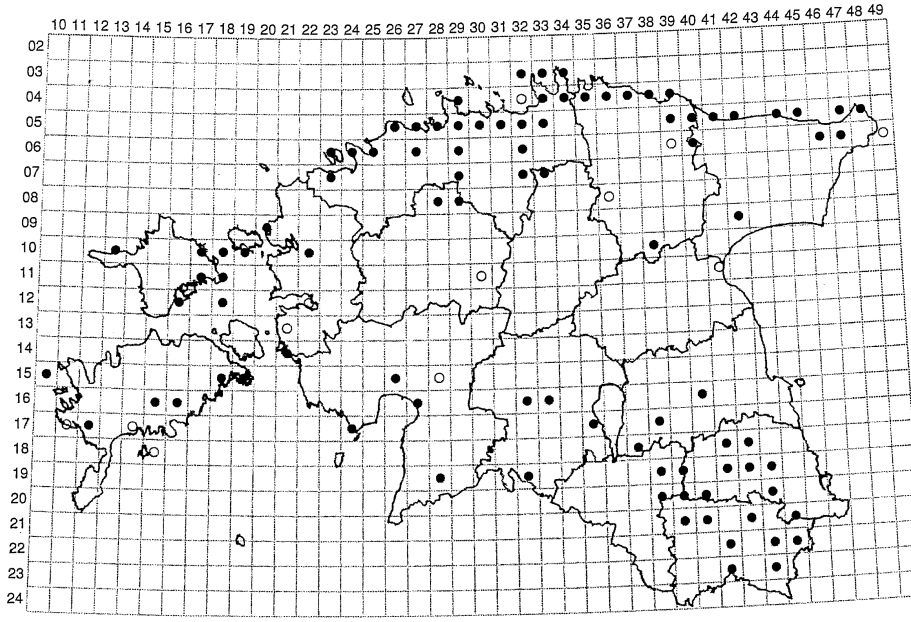

Fig. 2. The distribution of *Corydalis solida* in Estonia in 1921–2005 is displayed in a grid of 9 × 11 km squares. Empty circle: recorded in 1921–1970; filled circle: recorded in 1971–2005 (Kukk & Kull 2005).

ceived a lot of attention through the decades and is often recorded more carefully than common species. Therefore, we expect that presence of Clouded Apollo in certain areas would have been noticed whereas unrepresentative recording of *P. mnemosyne* especially in different locations is not the issue of this study. Additionally, there is no reason to doubt the study effort in the three regions of Estonia where the species is present. Since the area of the country is relatively small, practically the same amount of attention has been paid to butterfly research all over Estonia. It should be noted that the number of the lepidopterists has been almost the same through the times.

The general distribution pattern of Clouded Apollo in Estonia is in good agreement with the distribution of its larval host plant species. Interestingly, *C. solida* has not been recorded in central Estonia and most probably because of that the butterfly has neither been recorded there. Furthermore, this phenomenon offers a plausible explanation why the butterfly occupies three geographically separated areas in Estonia. Since there are rather long distances between these three regions and because the initial findings of the butterfly in the regions came from different years, we suggest that the colonisation of these three regions by Clouded Apollo took place from different directions. For instance, to North Estonia the butterfly probably expanded from Russia, to south-eastern Estonia from North-East Latvia or Russia (Pskov region) and to Saaremaa from western Latvia. This is supported by the general distribution areas of Clouded Apollo in neighbouring countries. However, there is no certain evidence for this interpretation and further investigation to clarify this is needed.

The results of this study showed that the specialist species Clouded Apollo has increased its abundance and distribution in Estonia. The general trend for most European grassland butterflies and also elsewhere for *P. mnemosyne*, is a decline in abundance and distribution area (Kuussaari *et al.* 2007, Settele *et al.* 2008). Habitat loss, deterioration of habitat quality, increasing fragmentation of habitat patches or combined effects of all these factors are the main threats to Clouded Apollo (Meglécz *et al.* 1999, Luoto *et al.* 2001,

Bergström 2005). In Estonia, the extinction of the subspecies of Saaremaa Island has most likely been related to habitat degradation in particular locations and a lack of other suitable habitats in the vicinity. Therefore, a possible explanation of the pattern of contrasting trends of Clouded Apollo in different geographical regions is availability and quality of suitable habitats. Similarly to other European countries, the traditional extensive agricultural practice is decreasing in Estonia. In general, the area of semi-natural grasslands in Estonia has decreased from 1,571,000 ha in 1939 to 130,000 ha in 2006 (Kukk & Sammul 2006). However, the area of specific semi-natural grasslands that are suitable habitats for Clouded Apollo still remains high. This is particularly notable in the case of semi-natural riparian meadows with strips of alders that are the preferred habitat for *C. solida* and Clouded Apollo in Estonia (Meier *et al.* 2005). Therefore, the increasing occupancy trend of Clouded Apollo observed in recent decades is likely to be associated with the fact that there is still a good availability of semi-natural grasslands, which are suitable for the butterfly. Additionally, Estonia has a good ecological network of natural communities and corridors, especially along rivers with riparian meadows that support the dispersal of Clouded Apollo. However, many suitable semi-natural grasslands are abandoned and have high risk of forest overgrowth, which could lead to higher pressure to the populations of Clouded Apollo in the future.

5. Conclusions

In this study, we provided an overview of the distribution of the threatened butterfly Clouded Apollo (*Parnassius mnemosyne*) in Estonia. During the last 30 years, the abundance and distribution area of Clouded Apollo has increased, except the subspecies on the island of Saaremaa has most probably gone extinct. On the other hand, a new record came from south-eastern Estonia in 1984, where the species had not been found previously. The exact reasons for the increase are unclear, but one can assume that the tendency is a combination of several factors, such as the presence of suitable habitats for the butterfly, the appropriate landscape structure with a sufficient density of habitat patches that support the dispersal of the butterfly. However, specific attention should be paid to avoiding the disappearance of suitable habitats of Clouded Apollo in the future.

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References

Aagaard, K. & Hansen, O. 1992: Population studies of *Parnassius mnemosyne* (Lepidoptera) in Sunndalen, Norway. — In: Pavlicek, T., Ovaa, A. H. & van der Made, J. G. (eds), Future of Butterflies in Europe: strategies for survival. Proceedings of the International Congress, held at Wageningen during April 12–15, 1989: 160–166. Agricultural University Wageningen, Wageningen. 326 pp.

Bergström, A. 2005: Oviposition site preferences of the threatened butterfly *Parnassius mnemosyne* – implications for conservation. — Journal of Insect Conservation 9: 21–27.

Bryk, F. 1922: "Parnassiana". *Parnassius mnemosyne* L. in Europa. Die estnische Form. — Societas Entomologica 37: 5–6.

Gorbach, V. V. & Kabanen, D. N. 2010: Spatial Organization of the Clouded Apollo Population (*Parnassius mnemosyne*) in Onega Lake Basin. — Entomological Review 90: 11–22.

Gratton, P., Konopinski, K. & Sbordoni, V. 2008: Pleistocene evolutionary history of the Clouded Apollo (*Parnassius mnemosyne*): genetic signatures of climate cycles and a time-dependent mitochondrial substitution rate. — Molecular Ecology 17: 4248–4262.

Kesküla, T. 1989: Has *Parnassius mnemosyne* become extinct in Saaremaa Island? — Eesti Loodus 3: 154. [In Estonian.]

Kesküla, T. & Luig, J. 1997: Phenology and distribution of the Clouded Apollo *Parnassius mnemosyne* (Linnaeus, 1758) in Estonia, with the description of a new subspecies from south-eastern Estonia. — Atalanta 28: 17–20.

Konvička, M. & Kuras, T. 1999: Population structure, behaviour and selection of oviposition sites of an endangered butterfly, *Parnassius mnemosyne*, in Litovelské Pomoraví, Czech Republic. — Journal of Insect Conservation 3: 211–223.

Kukk, T. & Kull, T. 2005: Atlas of the Estonian Flora. — Eesti Maaülikooli Kirjastus, Tartu. 500 pp. [In Estonian.]

Kukk, T. & Sammul, M. 2006: Area of seminatural Natura 2000 habitat types in Estonia. — Eesti Looduseuurijate Seltsi aastaraamat 84: 114–159. [In Estonian.]

Kuussaari, M., Heliölä, J., Pöyry, J. & Saarinen, K. 2007: Contrasting trends of butterfly species preferring semi-natural grasslands, field margins and forest edges in northern Europe. — Journal of Insect Conservation 11: 351–366.

Luoto, M., Kuussaari, M., Rita, H., Salminen, J. & von Bonsdorff, T. 2001: Determinants of distribution and abundance in the clouded apollo butterfly: a landscape ecological approach. — Ecography 24: 601–617.

Meglécz, E., Nève, G., Pecsenye, K. & Varga, Z. 1999: Genetic variation in space and in time in *Parnassius mnemosyne* (L.) (Lepidoptera) populations in north-east Hungary: implications for conservation. — Biological Conservation 89: 251–259.

Meier, K., Kuusemets, V., Luig, J. & Mander, Ü. 2005: Riparian buffer zones as elements of ecological networks: Case study on *Parnassius mnemosyne* distribution in Estonia. — Ecological Engineering 24: 531–537.

Settele, J., Kudrna, O., Harpke, A., Kuhn, I., van Swaay, C., Verovnik, R., Warren, M., Wiemers, M., Hanspach, J., Hickler, T., Kuhn, E., van Halder, I., Veling, K., Vliegenthart, A., Wynhoff, I. & Schweiger, O. 2008: Climatic Risk Atlas of European Butterflies. — BioRisk 1: 1–710.

Van Swaay, C., Cuttelod, A., Collins, S., Maes, D., López Munguira, M., Šašić, M., Settele, J., Verovnik, R., Verstrael, T., Warren, M., Wiemers, M. & Wynhof, I. 2010: European Red List of Butterflies. Publications Office of the European Union. Luxembourg. 48 pp.

Viidalepp, J. 2000: Clouded Apollo (*Parnassius mnemosyne*) in Estonia. — Teaduste Akadeemia Kirjastus, Tallinn–Tartu. 40 pp. [In Estonian.]

Väisänen, R. & Somerma, P. 1985: The status of *Parnassius mnemosyne* (Lepidoptera, Papilionidae) in Finland. — Notulae Entomologicae 65: 109–118.

Välimäki, P. & Itämies, J. 2003: Migration of the clouded Apollo butterfly *Parnassius mnemosyne* in a network of suitable habitats – effects of patch characteristics. — Ecography 26: 679–691.

Kuusemets, V., Meier, K., Luig, J. & **Liivamägi, A.** 2005.
HABITAT AND LANDSCAPE STRUCTURE OF CLOUDED APOLLO (*PARNASSIUS MNEMOSYNE*)
Kuchn, E., Thomas, J., Feldmann, R. & Settele, J. (Eds.) Studies on the Ecology and Conservation of Butterflies in Europe. Vol.1. General Concepts and Case Studies. Pensoft Publishers, Sofia-Moscow, p 18-21.

E. Kuehn, J. Thomas, R. Feldmann & J. Settele (Eds) 2005
Studies on the Ecology and Conservation of Butterflies in Europe
Proceedings of the Conference held in UFZ Leipzig, 5-9th of December, 2005, pp. 00-00

Habitat and landscape structure requirements of Clouded Apollo (*Parnassius mnemosyne*)

Valdo Kuusemets[1], Kadri Meier[1], Jaan Luig[2] & Ave Liivamägi[3]

[1] Estonian Agricultural University, Institute of Agricultural and Environmental Sciences, Kreutzwaldi 5, Tartu 51014, Estonia
[2] University of Tartu, Institute of Zoology and Hydrobiology, Estonia
[3] University of Tartu, Institute of Geography, Estonia
Contacts: valdo.kuusemets@eau.ee

INTRODUCTION

The Clouded Apollo (*Parnassius mnemosyne*), a protected species by EU Directive *Natura* 2000, has special habitat requirements. The larva of the Clouded Apollo is dependent on the leaves of a single plant species (*Corydalis solida*). This plant grows along sunny margins of forests and trees where the soil is moist, but not in permanently flooded places, wetlands and hummocks. Therefore, the fumewort grows mainly in river valleys with strips of trees, in floodplains and in wooded meadows.

The adult of the Clouded Apollo requires open meadows that are its mating place and the habitat for the food nectar plants (Meglécz et al., 1999). The study in Finland (Luoto et al., 2001) showed that the presence of Clouded Apollo was significantly dependent on the number of fumewort, on the heterogeneity of landscapes, and on the presence of semi-natural grasslands, deep valleys and areas with low wind speed. At the same time the dispersal distances between habitat patches are short, which means that a dense habitat network is needed for conservation of this species (Välimäki and Itämies, 2003). These kinds of conditions are met in riparian communities of rivers, especially in strips with bushes and trees that propote migration of the Clouded Apollo. Also, in Estonia the Clouded Apollo has been mainly found in riparian meadows with a strip of bushes and trees that are habitats for suitable plants, which provide warmer, sheltered places (Viidalepp, 2000).

METHODS

All known locations and descriptions of Clouded Apollo (*Parnassius mnemosyne*) in Estonia were collected and standardised. A uniform database with GIS was formed using MapInfo Professional 6.5, observation of a Clouded Apollo was linked with its location on the digital cadastral map of Estonia (1:10 000). The analysis of the land cover and plant community types of habitats of Clouded Apollo was made on the basis of the digital cadastral map. For analysis, only these data were used, where it was possible to determine the exact location of the Clouded Apollo on the cadastral

map. Also, descriptions from before 1980 were excluded, since the land cover and habitat type on the cadastral map could not respond to the situation when the butterfly was found.

In June 2003, a detailed survey of Clouded Apollo was made along the River Ahja. The number and sex of butterflies was estimated, the habitat description (dominant plants, presence of bushes close to river, land use) was made. At the end of April, all findings of fumewort were marked to the cadastral map.

RESULTS

There were 116 reports of Clouded Apollo from 1903 to 2002 in Estonia. Most of them (85; 73%) are from the period post-1990, in the 1980-s there were 12(10%) and from the earlier period 19(16%) records. There are three main centres of Clouded Apollo in Estonia: the population of the island of Saaremaa, and the North-Estonian and the South-Estonian populations (Figure 1). The Saaremaa population has not been recorded since 1973 and is probably extinct. The first description of Clouded Apollo in North-Estonia was made in 1903. During the first half of the last century, all records were confined to the very east of North-Estonia. Later the species expanded to the west and, especially during the last 10 years, has been found in the valleys of several North-Estonian rivers.

The South-Estonian population was first described in 1985 but has been increasing rapidly in territory and in the number of individuals. Despite the fact that the Clouded Apollo is decreasing in most areas of Europe (Meglécz et al., 1999), the population area and number of individuals is increasing at the Northern boundary of the population. Results show that there is an overall increase in the number of Clouded Apolloa in Estonia, with 73% of all sighting having been made during the last 13 years. The exact reasons for this increase in Estonia are unclear but one precondition is the presence of suitable habitats for the butterfly (Meier et al., 2005).

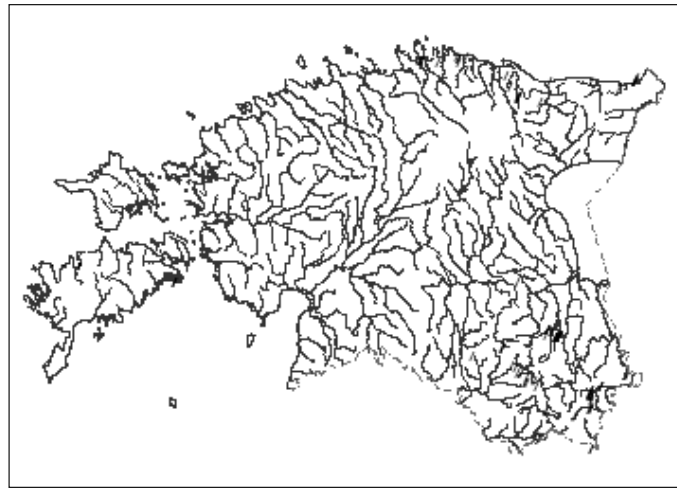

Fig. 1. The river network and distribution of Clouded Apollo (*Parnassius mnemosyne*) in Estonia.

From all findings of Clouded Apollo, 15(13%) have been located on the banks of lakes, 10(9%) on the coastal area of the Baltic Sea and all the rest (91; 78%) on the riparian areas of the rivers. The dominating land cover type was meadow with riparian strips of bushes and trees close to the riverbank. This habitat type was found in about 60% of described sites of Clouded Apollo. 30% constituted meadows and 10% wet meadows that were predominantly situated between meadows with riparian bushes (Meier et al., 2005).

Our detailed study showed, that the Clouded Apollo is mainly related to meadow with riparian strip of bushes and trees especially with grey alder (*Alnus incana*) (Figure 2). This is a typical riparian tree in Estonia, whereas the under floor of narrow riparian alder strip close to water table is the main habitat for fumeworts. Therefore, the Clouded Apollo is mainly found in the dry riparian meadows with alder strip while this habitat is the main habitat of the food plant of the larvae of Clouded Apollo, while this habitat is the main feeding and mating place of adult and while this habitat provides suitable migration and hiding place for the adult of the butterfly. This kind of habitat is linked to traditional agricultural practices in Estonia, like hay making and grazing of cattle and sheep. However, during last years this agricultural practice is considerably decreased and former meadows are overgrowing. There is also pressure to cut down riparian bushes and trees. All can lead to the loss of habitats of Clouded Apollo.

Findings of Clouded Apollo are mainly situated along the banks of rivers. Rivers with riparian strips of bushes form suitable migration corridors for Clouded Apollo and provide habitat patches in the riparian meadows. The appropriate density of habitat patches and existence of migration corridors create appropriate landscape structure for dispersal and survival of butterfly avoiding its fragmentation and disappearance.

Therefore, the conservation of Clouded Apollo should consider its habitat requirements and general landscape structure to ensure all ecological needs of this butterfly.

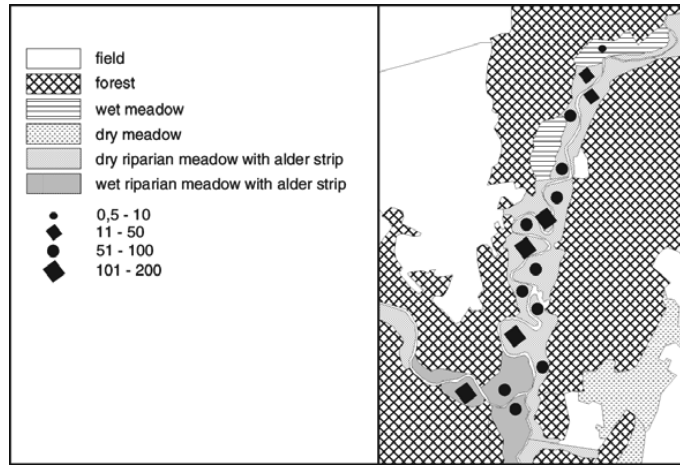

Fig. 2. Habitat type structure and density (individuals per hectare) of Clouded Apollo (*Parnassius mnemosyne*) in the Ahja River valley, South Estonia.

CONCLUSIONS

- The number of Clouded Apollo has increased in recent years in Estonia. There is a new population with a high number of individuals in South-Estonia.
- The larvae and imago of Clouded Apollo require specific habitat – riparian meadow with strips of bushes, that is typical for traditional agricultural landscapes (hay making, grazing), which have nowadays a high risk of being abandoned and overgrown by bushes and trees.
- Rivers with riparian strips of trees and meadows are creating suitable landscape structure for the migration and survival of the Clouded Apollo.
- The protection of Clouded Apollo needs protection of the riparian habitat that should be managed in traditional ways, as well as and the preservation of riparian strips of bushes and trees to preserve multifunctional ecologically balanced landscapes.

REFERENCES

Luoto, M., Kuussaari, M., Rita, H., Salminen, J., von Bonsdorff, T., 2001. Determinants of distribution and abundance in the clouded Apollo butterfly: a landscape ecological approach. Ecography, 24(5), 601-617.

Meglécz, E., Nève, G., Pecsenye, K., Varga, Z., 1999. Genetic variations in space and time in *Parnassium mnemosyne* (L.) (Lepidoptera) populations in north-east Hungary: implications for conservation. Biological Conservation, 89, 251-259.

Meier, K., Kuusemets, V., Luig, J., 2005. Riparian buffer zones as elements of ecological networks: Case study on *Parnassius mnemosyne* distribution in Estonia. Ecological Engineering, 24, 531-537.

Viidalepp, J., 2000. Clouded Apollo (*Parnassius mnemosyne*) in Estonia (in Estonian). Tallinn-Tartu, pp. 40.

Välimäki, P., Itämies, J., 2003. Migration of the clouded Apollo butterfly *Parnassius mnemosyne* in a network of suitable habitats – effects of patch characteristics. Ecography, 26, 679-691.

CURRICULUM VITAE

Personal information

Name:	Ave Liivamägi
Date and place of birth:	November 19th, 1981, Jõgeva
Address:	Härjanurme village, Puurmani Parish, Jõgeva County
E-mail:	ave.liivamagi@emu.ee

Education

2006-2013	PhD studies in Environmental Sciences and Applied Biology, Estonian University of Life Sciences
2000-2006	BSc studies in Geography and Landscape Ecology, and teacher of Geography, University of Tartu

Additional training

NOVA PhD course "Insect Conservation". Oscarsborg, Norway

Academic degree

Baccalaureus scientiarum degree in Geography and Landscape Ecology

Languages

Estonian (Mother tongue),
English (Intermediate level)

Professional employment

since 2012	Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences, Researcher
2012-2013	University of Tartu, Institute of Ecology and Earth Sciences, Environmental Specialist
2010-2012	The Environmental Board, Mineral Resources, Water and Air Pollution Specialist
2008-2012	Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences, Technician

2005-2007	Luua Forestry School, Teacher
2005-2007	Saduküla Basic School, Teacher

Field of research

Landscape ecology, pollinating insect conservation

Awards and grants

2009	ESF DoRa T8 "Participation of young researches in international exchange of knowledge" – NOVA PhD course on Insect Conservation, Norway

Projects

01.01.2012-31.12.2014	8-2/T12056PKKS, "Dynamics of living systems in the context of nature preservation"
01.01.2012-12.12.2013	SLOOM12006, "Buffer zones to limit and mitigate harmful effects of long-term anthropogenic influence to maintain ecological functionality of bogs"
24.01.2008-01.12.2010	8-2/T8014PKPK, "Ecological and landscape requirements of semi-natural habitats and their sustainable management "
01.01.2007-31.12.2012	SF1090050s07, "Biotic and abiotic markers for the evaluation of complex anthropogenic influences on habitats and landscapes"

ELULOOKIRJELDUS

Isikuandmed

Nimi:	Ave Liivamägi
Sünniaeg ja koht:	19. november 1981, Jõgeva
Aadress:	Härjanurme küla, Puurmani vald, Jõgeva maakond
E-post:	ave.liivamagi@emu.ee

Haridustee

2006-2014	Doktoriõpe keskkonnateaduse ja rakendusbioloogia erialal, Eesti Maaülikool
2000-2006	Bakalaureuseõpe loodusgeograafia ja maastikuökoloogia erialal ning põhikooli ja gümnaasiumi geograafiaõpetaja õpetajakoolitus, Tartu Ülikool

Erialane täiendamine

2009	NOVA doktorikursus "Insect Conservation", Oscarsborg, Norra

Teaduskraad

*Baccalaureus scientiarum*i kraad loodusgeograafia ja maastikuökoloogia erialal

Keelteoskus

Eesti keel (emakeel),
Inglise keel (kesktase)

Teenistuskäik

alates 2012	Põllumajandus- ja Keskkonnainstituut, Eesti Maaülikool, nimetatud teadur
2012-2013	Ökoloogia ja Maateaduste Instituut, Tartu Ülikool, keskkonnaspetsialist
2010-2012	Keskkonnaamet, maavarade, vee ja välisõhu spetsialist
2008-2012	Põllumajandus- ja Keskkonnainstituut, Eesti Maaülikool, tehnik

2005-2007	Luua Metsanduskool, geograafiaõpetaja
2005-2007	Saduküla Põhikool, bioloogia- ja loodusõpetuse õpetaja

Uurimistöö põhisuunad

Maastikuökoloogia, tolmeldajate kaitse

Teaduspreemiad ja stipendiumid

ESF DoRa T8 reisistipendium doktorikoolis osalemiseks: NOVA doktorikursus "Insect Conservation", Norras

Teadustegevus (projektid)

01.01.2012-31.12.2014	8-2/T12056PKKS, "Elussüsteemide dünaamika loodushoiu kontekstis"
01.01.2012-12.12.2013	SLOOM12006, "Soode ökoloogilise funktsionaalsuse tagamiseks vajalike puhvertsoonide määratlemine pikaajaliste häiringute leviku piiramiseks või leevendamiseks"
24.01.2008-01.12.2010	8-2/T8014PKPK, "Pärandkoosluste ökoloogilised ja maastikulised nõudlused ning nende säästlik majandamine"
01.01.2007-31.12.2012	SF1090050s07, "Antropogeensed mõjud biotoopidele ja maastikele: biootilised ja abiootilised markerid"

LIST OF PUBLICATIONS

Publications indexed in the ISI Web of Science database

Liivamägi, A., Kuusemets, V., Luig, J. & Kask, K. 2013. Changes in the distribution of Clouded Apollo *Parnassius mnemosyne* (Lepidoptera: Papilionidae) in Estonia. Entomologica Fennica 24 (3): 186-192.

Diaz-Forero, I., Kuusemets, V., Mänd, M., Liivamägi, A., Kaart, T. & Luig, J. 2013. Influence of local and landscape factors on bumblebees in semi-natural meadows: a multiple-scale study in a forested landscape. Journal of Insect Conservation 17 (1): 113-125.

Diaz-Forero, I., Kuusemets, V., Mänd, M., Liivamägi, A., Kaart, T. & Luig, J. 2011. Effects of forest habitats on the local abundance of bumblebee species: a landscape-scale study. Baltic Forestry 17 (2): 235-242.

Peer-reviewed articles in other international research journals

Diaz-Forero, I., Liivamägi, A., Kuusemets, V. & Luig, J. 2010. Pollinator richness and abundance in Northeast Estonia: bumblebees, butterflies and day-flying moths. Forestry Studies | Metsanduslikud Uurimused 53: 5-14.

Conference abstracts

Liivamägi, A., Kuusemets, V., Kask, K. & Luig, J. 2012. Changes of the spatial distribution and habitat requirements of Clouded Apollo (*Parnassius mnemosyne*) in Estonia. International Symposium: Future of Butterflies in Europe III, March 29-31, Wageningen, the Netherlands.

Luig, J., Liivamägi, A., Kask, K. & Kuusemets, V. 2012. The distribution changes and threats of butterflies in Estonia. International Symposium: Future of Butterflies in Europe III, March 29-31, Wageningen, the Netherlands.

Diaz-Forero, I., Liivamägi, A., Kuusemets, V. and Luig, J. 2010. How are habitat and landscape factors influencing the diversity and abundance of bumblebees? Conference "Nature Conservation beyond 2010", May 27-29, Tallinn, Estonia.

Liivamägi, A., Kuusemets, V., Luig, J. and Kask, K. 2009. State of art of Estonian EU Directive Natura 2000 butterfly species. 2nd European Congress of Conservation Biology "Conservation biology and beyond: from science to practice", September 1-5, Prague Czech Republic.

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